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# Latest Paleocene to earliest Eocene bryozoans from Chatham Island, New Zealand

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## CONTENTS

**SYNOPSIS.** Named bryozoans have not previously been recorded from the New Zealand Paleocene or earliest Eocene. We here describe 42 species, 21 new, from the Red Bluff Tuff of Waipawan age (latest Thanetian to earliest Ypresian) collected from Pukekio, Chatham Island, New Zealand. Twelve of the species are cyclostomes, one is a ctenostome boring, and 29 are cheilostomes. Three genera are new – *Melychocella*, *Smitticellaria* (Cellariidae) and *Chataimulosia* (Buffonellodidae), the latter comprising the earliest occurrence of the Buffonellodidae, the only family in the collection representative of a 'cryptocystidean' frontal shield. The following species are new: *Cinctipora solomoni*, *Ceriopora rekohuensis*, *Flustrellaria australis*, *Akatopora chathamica*, *Micropora quadriporosa*, *Inversaria gondwanae*, *Chondriovelum fossilis*, *Ogiva incompta*, *Onychocella*? *lamellosa*, *Aspidostoma litotes*, *A. cinnabarina*, *Cellaria minus*, *C. perexigua*, *C. elementaria*, *Smitticellaria morioriana*, *Melychocella cynura*, *Arachnopusia gracilis*, *Hippopleurifera australis*, *Exochella*? *gracilis*, *Escharoides*? *crassa* and *Chataimulosia primaeva*. Forward range extensions include *Flustrellaria*, *Inversaria*, and possibly *Escharicellaria* and *Pavobeisselina*. Backward range extensions include unequivocal *Cinctipora* and Cinctiporidae, and *Akatopora*. Newly recorded for the southern hemisphere are *Flustrellaria*, *Inversaria*, *Hippopleurifera*, and possibly *Hoplitaechmella*, *Escharicellaria*, and *Pavobeisselina*. The overall taxonomic character of the bryofauna is mixed, both geographically and temporally, with genera reminiscent of northern hemisphere Maastrichtian and Danian bryofaunas co-occurring with families like Arachnopusiidae and Romancheinidae that are common in Neogene and Recent southern hemisphere bryofaunas.

## INTRODUCTION

This is the first of a projected series of publications intended formally to describe the Cenozoic Bryozoa of New Zealand. The last, and only, major monograph of New Zealand Cenozoic bryozoans was that of Brown (1952): *The Tertiary cheilostomatous Polyzoa of New Zealand*, a seminal work for the study of New Zealand bryozoans, including living faunas. The title notwithstanding, Brown's material also included Pleistocene specimens then regarded as Pliocene in age. Further, no material older than Oligocene was studied, so the rich Eocene bryofaunas of the Oamaru District and Chatham Islands have remained neglected until very recently, when two species of Catenicellidae were described (Gordon & Braga 1994), and virtually nothing has been reported from the Paleocene.

The Paleocene in New Zealand is represented by the local Teurian Stage, deposits of which are widespread but thin. With the exception of two well-known early Teurian (= Danian) localities at Wangaloa and Boulder Hill, eastern Otago, Teurian rocks are almost devoid of microfossils. Bryozoa (undescribed) have been recorded from only one mainland Paleocene locality, the Kauru Formation near Oamaru (Stilwell *et al.*, 1994), where they are reportedly abundant, and latest Paleocene bryozoans are richly represented in parts of the Red Bluff Tuff on the Chatham Islands (Campbell *et al.*, 1993).

New Zealand Paleocene bryozoans potentially have considerable evolutionary interest. Whereas Maastrichtian bryofaunas are known from several parts of the world, Paleocene faunas are much rarer (MacLeod *et al.*, 1997), and limited knowledge of bryozoan systematics and stratigraphy across the K-T boundary hampers interpretations of extinction and survival which have relied almost entirely on evidence from northern European localities (e.g., McKinney *et al.*, 1998). Studies of European and North American Cretaceous and Paleocene Bryozoa have shown that, although numerous Maastrichtian taxa disappeared at the K-T boundary, a number of genera and species persisted into the Danian (Voigt 1985a; Viskova & Weiss 1998). In fact, the Danian is notable for the relative paucity of taxonomic novelty among Bryozoa, and this is true also of the Thanetian. By contrast, there is a spectacular Ypresian diversification of Bryozoa, including higher taxonomic levels (families and genera) (Voigt 1985a; Taylor 1993; Gordon & Voigt 1996). Indeed, Voigt (1985a) regarded the Danian as taxonomically the last stage of the Cretaceous for Bryozoa. The reasons for taxonomic conservatism among Paleocene bryozoans are unclear, especially since frontal-shield evolution in Late Cretaceous cheilostomes appears to have resulted in innovative morphological characters (most notably the ascophorine ascus and hypostegal coelom) that predominate in Eocene taxa (Gordon & Voigt 1996). A macroevolutionary lag in recovery following the K-T extinction event is one possibility, but the relative paucity of Paleocene bryofaunas compared to later Eocene ones may accentuate the contrast.

Here, we describe a bryozoan fauna of 42 species from the latest Paleocene to earliest Eocene Red Bluff Tuff on Chatham Island, New Zealand. Apart from a study of Argentinian bryozoans of the Roca Formation early this century (Canu 1911) and that of Brood (1976) on a Madagascan fauna, no other Paleocene bryozoans have been reported from the Southern Hemisphere. Consequently, the fauna reported here helps to fill a major gap in our knowledge of the taxonomy, stratigraphy, and palaeobiogeography of early Palaeogene Bryozoa.

## GEOLOGICAL SETTING

The Chatham Islands form a small archipelago located some 850 km east of the South Island of New Zealand, at the eastern end of the Chatham Rise, a submarine extension of the New Zealand subcontinent (Fig. 1). The two largest islands – Chatham Island and Pitt Island – are populated. The geology of the Chathams has been comprehensively described by Campbell *et al.* (1993). A pre-mid-Cretaceous basement of metamorphic rocks (Chatham Schist) is overlain by a sequence of Cretaceous and Cenozoic sedimentary, volcanic and volcaniclastic rocks. Many of the sedimentary units are richly fossiliferous, and include several cool-water limestones dominated by bryozoans, foraminifera and molluscs.

The Red Bluff Tuff is described by Campbell *et al.* (1993: 74) as '. . . a predominantly calcareous palagonite tuff of basaltic composition, with beds of lapillistone and tuff-breccia'. Widely distributed on both Chatham and Pitt Islands, at most localities it is a brick-red to yellow-brown colour, except for the lower parts which are dark green and grey-brown, and is generally well bedded with cross-bedding, graded bedding, and other evidence of water sorting

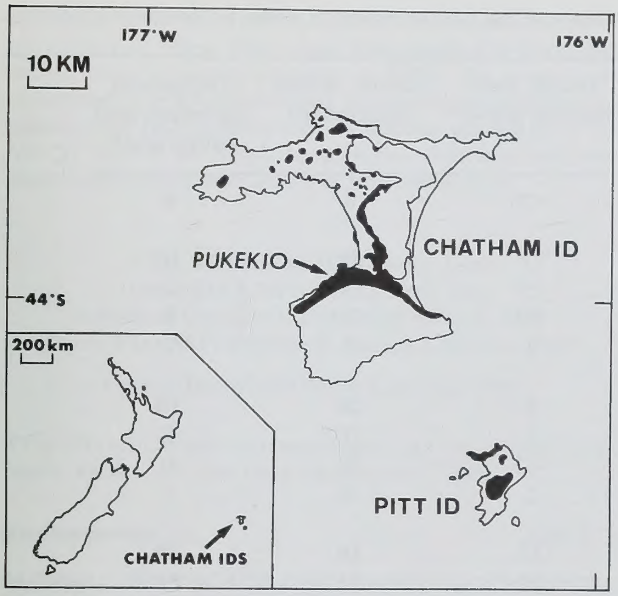


**Fig. 1** Simplified map of the Chatham Islands with the distribution of the Kekerione Group (Paleocene-Miocene), which includes the Red Bluff Tuff, marked in black (redrawn from Campbell *et al.*, 1993: fig. 4.35) and the bryozoan locality Pukekio indicated. Inset map shows the position of the Chatham Islands relative to the mainland of New Zealand.

(Campbell *et al.*, 1993). At several localities (Waihere Bay on Pitt Island, Red Bluff and the coast south of Point Weeding to Pukekio Hill on Chatham island) the formation is reasonably accessible and can exceed 50 m in thickness. In high land south of Lake Huro it is around 100 m thick.

The Red Bluff Tuff is a fossiliferous and largely marine unit belonging to the Kekerione Group. Fossil content includes spores, pollen, foraminifera, calcareous nannofossils, sponges, corals, bryozoans, brachiopods, bivalves, gastropods, nautiloids, barnacles, echinoderms, vertebrates (teeth), and trace fossils, with epifaunal assemblages dominating (Campbell *et al.*, 1993). Though reported as being present, the Bryozoa of the Red Bluff Tuff have never been described. The collection described here was made during a recent (February 1997) palaeontological expedition to the Chatham Islands (see Acknowledgments) and comes from Pukekio (Fig. 1), south-west of the radio station near Waitangi on the main Chatham Island (NZMS 260 Chatham Islands 1: 50 000 topographical map, 1981, grid reference 432540). The locality is New Zealand Fossil Record CH/f477. Determinations of foraminifera from Pukekio show the lower part of the formation to be late Teurian (= mid-Thanetian). The middle part of the formation ranges from early to late Waipawan (= latest Thanetian to earliest Ypresian). Whereas stratigraphy, cross-bedding, and textural characters suggest shallow-marine depositional conditions, fossil evidence is said to indicate mid-shelf to upper bathyal environments (Campbell *et al.*, 1993).

## COLONIAL MORPHOLOGY AND PALAEOECOLOGY

Listed below are the 42 bryozoan species found in the Red Bluff Tuff with their colonial morphologies.

| | |
|---|---|
| **Cyclostomata** | |
| *Stomatoporina* sp. | encrusting, runner |
| ?*Oncousoecia* sp. | encrusting, runner |
| '*Berenicea*' sp. | encrusting, patch/sheet |
| ?*Idmidronea* sp. | fixed-erect, planar tree |
| 'Entalophorid' sp. | fixed-erect, tree-like |
| ?*Attinopora* sp. | fixed-erect, tree-like |
| *Cinctipora solomoni* sp. nov. | fixed-erect, tree-like |
| Erect tubuliporine base sp. 1 | fixed-erect, ?tree-like |
| Erect tubuliporine base sp. 2 | fixed-erect, ?tree-like |
| *Ceriopora rekohuensis* sp. nov. | encrusting, mound |
| ?*Tetrocycloecia* sp. | fixed-erect, tree-like |
| *Disporella* sp. | encrusting, patch |
| **Ctenostomata** | |
| *Immergentia* sp. | shell-boring, runner |
| **Cheilostomata** | |
| *Flustrellaria australis* sp. nov. | encrusting, patch/sheet |
| *Akatopora chathamica* sp. nov. | encrusting, patch/sheet |
| *Caleschara* sp. | encrusting, patch/sheet multilamellar |
| *Micropora quadriporosa* sp. nov. | encrusting, patch |
| ?*Hoplitaechmella* sp. | encrusting, patch |
| Microporid sp. | ?fixed-erect, ?rod/?planar tree |
| *Inversaria gondwanae* sp. nov. | fixed-erect, tree-like |
| *Chondriovelum fossilis* sp. nov. | ?fixed-erect, tree-like |
| *Ogiva incompta* sp. nov. | ?fixed-erect, planar tree |
| *Onychocella*? *lamellosa* sp. nov. | encrusting, patch/sheet/mound/multilamellar |
| ?*Onychocella* sp. | encrusting, patch/sheet |
| Onychocellid sp. | ?encrusting, ?patch/sheet |
| *Aspidostoma litotes* sp. nov. | fixed-erect, ?tree-like |
| *Aspidostoma cinnabarina* sp. nov. | encrusting, patch/sheet |
| *Cellaria minus* sp. nov. | flexible-erect, tree-like |
| *Cellaria perexigua* sp. nov. | flexible-erect, tree-like |
| *Cellaria elementaria* sp. nov. | flexible-erect, tree-like |
| *Cellaria* aff. *depressa* Maplestone | flexible-erect, tree-like |
| *Smitticellaria morioriana* sp. nov. | ?flexible-erect, planar tree |
| ?*Escharicellaria* sp. | ?flexible-erect, planar tree |
| *Melychocella cynura* sp. nov. | ?flexible-erect, ?rod/?planar tree |
| *Arachnopusia gracilis* sp. nov. | fixed-erect, ?rod/?planar tree |
| ?*Pavobeisselina* sp. | rooted, lobate |
| *Hippopleurifera australis* sp. nov. | encrusting, patch/sheet |
| *Exochella*? *gracilis* sp. nov. | fixed-erect, ?rod/planar tree |
| *Escharoides*? *crassa* sp. nov. | encrusting, patch/sheet |
| Lepraliellid sp. 1 | encrusting, patch/sheet |
| ?Lepraliellid sp. 2 | self-encrusting, free, multilamellar |
| *Chataimulosia primaeva* sp. nov. | encrusting, patch/sheet |

There is some margin of error in interpreting colonial morphologies owing to the incompleteness of colony fragments. Almost 50% of the 42 species are surface encrusters, predominantly those forming more-or-less circular patches or sheets. Only ca. 7% (excluding the shell-boring species) of the fauna consists of ramifying, runner-like colonies. Some 46% of the fauna are erect species, of which slightly less than half were probably basally rooted, allowing for bending of whole colonies in a current. The proportional representation of colonial morphologies in the Red Bluff Tuff fauna can be compared with bryofaunas from other settings (Table 1).

Although encrusters dominate taxonomically the bryofauna in the

**Table 1** Percentage occurrences of different bryozoan colony morphologies in different settings based on numbers of species, not numbers of colonies or colony fragments (* from Gordon (1987); † from Lee *et al.* (1997)).

| MORPHOLOGY | Red Bluff Tuff | Recent, shell gravel* | Recent, shell/ volcanic gravel* | Eocene, mobile rockground† | Terrigenous, carbonate mud (deep sea)* |
|---|---|---|---|---|---|
| **Shell-boring** | **2** | **0** | **<1** | **0** | **0** |
| **Total encrusting** | **50** | **72** | **77** | **59** | **10** |
| runner | 7 | 6 | 15 | 7 | 0 |
| patch | 38 | 61 | 59 | 50 | 8 |
| mound | 5 | 5 | 3 | 2 | 2 |
| **Total fixed-erect** | **29** | **12** | **8** | **26** | **10** |
| tree | 22 | 8 | 6 | 26 | 8 |
| rod | 7 | 0 | <1 | 0 | 0 |
| lamellar | 0 | 4 | 2 | 0 | 2 |
| **Total flexible-erect** | **17** | **15** | **13** | **14** | **39** |
| tree | 17 | 15 | 13 | 13 | 31 |
| rod | 0 | 0 | 0 | 1 | 2 |
| lamellar | 0 | 0 | 0 | 0 | 6 |
| **Total dwarf-rooted** | **2** | **0** | **2** | **0** | **41** |
| conical | 0 | 0 | 2 | 0 | 33 |
| lobate | 2 | 0 | 0 | 0 | 4 |
| pedunculate | 0 | 0 | 0 | 0 | 4 |
| **Free-living** | **0** | **<1** | **0** | **1** | **0** |

Red Bluff Tuff at Pukekio (ca. 50% of all species), this proportion does not conform to the generalised pattern of modern bryozoan colonial morphologies on hard substrata around New Zealand. Gordon (1987) has shown that from a range of modern habitats, excluding the deep-sea and regardless of bryozoan diversity, the proportion of bryozoan species as planar or mounded encrusters of hard substrata is fairly consistent, ranging from 67–76% of the total bryofauna. This is a taxonomic measure, independent of actual numbers of colonies in each category, which are very difficult to obtain. The lower proportion of encrusting species in the Red Bluff Tuff samples could be correlated with the relative paucity of hard substrata (e.g., basaltic pebbles and cobbles, shell and other biogenic carbonate like stylasterid colonies). Alternatively, it may be a function of poor sampling. For Cenozoic cheilostome faunas in tropical America, Cheetham & Jackson (1998) have shown that encrusting species are far more numerous than erect or free-living species but have fewer occurrences per species and much less abundance per species. They are consequently the least well-sampled, and this may also be the case for the Red Bluff Tuff. The relative numbers of encrusting species at the Pukekio site is even less than that (59%) at Alma, Oamaru, where there is a notable mobile rockground dominated by bryozoans (Lee *et al.*, 1997). At the Alma site (and also at nearby Fortification Road, Kakanui) it is possible to count actual numbers of colonies because of the large numbers of lithoclasts, available for attachment in life, and the preservation of the bases of fixed-erect colonies. (Numbers of colonies of species that are articulated in life are impossible to determine owing to fragmentation.) The numbers of fixed-erect colony bases (mostly indeterminable to species but representing only 8 out of 301 bryozoan colonies counted) was significantly less than the numbers of fixed-erect species (20) represented in the Alma fauna and Fortification Road bryofauna from broken fragments found in the sieved sediment matrix between the clasts. Smith (1995) has summarised the range of taphonomic and other problems that confound palaeoecological reconstruction of bryozoan faunas, and these apply to the Red Bluff Tuff and Oamaru sites. One feature of the Red Bluff Tuff fauna may be noted, however – the unusually high number of cellariid species, including four species of *Cellaria*. Even accounting for taphonomic filters, this preponderance of *Cellaria* species at a single locality is truly noteworthy compared with later Cenozoic and Recent bryofaunas in New Zealand. Generally, the basally rooted, often articulated, erect colonies of cellariids are adapted to live in significant current speeds, as well as being able to tolerate moderate amounts of fine sedimentation (Lagaaij & Gautier 1965).

## SYSTEMATIC PALAEONTOLOGY

Specimen repositories and abbreviations: NHM, The Natural History Museum, London; IGNS, Institute of Geological & Nuclear Sciences (formerly New Zealand Geological Survey), Hutt City, New Zealand.

The species described were studied by scanning electron microscopy (SEM), using type and other specimens. Sorted material was soaked in hypochlorite solution overnight then washed in water while being subjected to light sonication. Cheilostomes and shelly specimens with boring ctenostomes were mostly gold-coated and imaged using secondary electrons at IGNS. The majority of cyclostomes were left uncoated and examined in an environmental chamber with back-scattered electron detector attached to an ISI ABT-55 SEM at the NHM. Morphometric determinations were made using eyepiece micrometres or from micrographs.

### Class **STENOLAEMATA** Borg, 1926
### Order **CYCLOSTOMATA** Busk, 1852
### Suborder **TUBULIPORINA** Milne Edwards, 1838
### Family **STOMATOPORIDAE** Pergens & Meunier, 1886

### Genus ***STOMATOPORINA*** Balavoine, 1958

TYPE SPECIES. *Alecto incurvata* Hincks, 1859, by original designation: Recent, U.K. (see Hayward & Ryland 1985).

### ***Stomatoporina*** sp. Figs 2, 3

MATERIAL. NHM BZ 4766, colony encrusting a pectinid bivalve shell.

DESCRIPTION. Colony encrusting, a narrow branch, about 5 mm long and 0.25–0.48 mm wide, initially uniserial and gently bowed, subsequently biserial and straight, lacking bifurcations but with beginnings of a single lateral ramification proximally; early astogenetic stages not preserved. Autozooids curved to left in uniserial part of branch, alternating in position of direction of curvature in biserial part; extent of frontal walls obscure, ridged distally, without preserved peristomes; apertures small, longitudinally elliptical, 0.06 × 0.04 mm, opening in a plane oblique to colony surface. Gonozooids absent. Kenozooids present at branch margins.

REMARKS. The sole specimen of this species is provisionally assigned to *Stomatoporina* on account of the curved proximal, uniserial branch with autozooids opening to one side and straight distal, biserial branch with autozooids opening alternately left and right. There is a particularly close resemblance in colony shape to a specimen of *S. spirata* (Walford) from the Jurassic of Dorset figured by Illies (1975, fig. 2a, pl. 1, fig. 6). Only three species of this Middle Jurassic (Bajocian) – Recent genus have been described (see Illies 1975; Hayward & Ryland 1985; Pitt & Taylor 1990), all from northern Europe. Therefore, the recognition of a probable *Stomatoporina* species in New Zealand greatly extends the known geographical range of the genus. More material is required before formally describing the species as new.

### Family **ONCOUSOECIIDAE** Canu, 1918

### Genus ***ONCOUSOECIA*** Canu, 1918

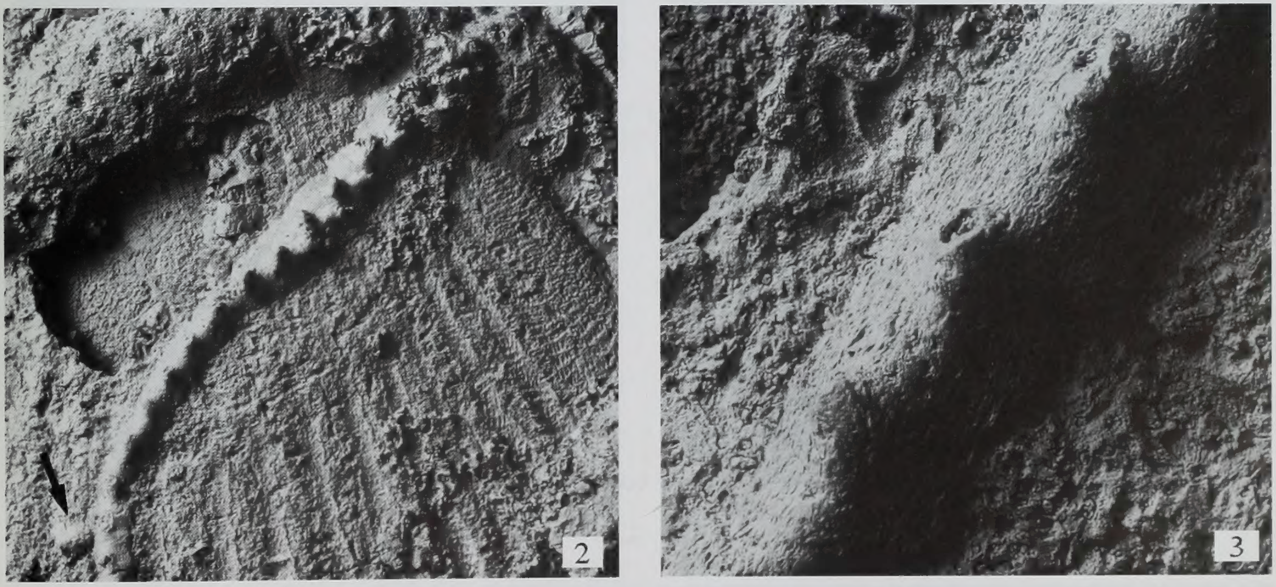
TYPE SPECIES. *Tubulipora lobulata* Hincks, 1880 (=*Alecto dilatans* Johnston, 1847; see Hastings 1963), by original designation; Recent, U.K.

### ?***Oncousoecia*** sp. [not figured]

MATERIAL. NHM BZ 4767.

DESCRIPTION. Colony small, fewer than 10 zooids being preserved, encrusting, initially uniserial, becoming bi- or triserial; ancestrula lacking or not identifiable. Autozooids with transversely elongate apertures about 0.10 mm long by 0.12 mm wide.

REMARKS. This small, immature colony lacks gonozooids and is therefore of highly uncertain affinity. However, the oligoserial zooids are reminiscent of some species of *Oncousoecia* to which the colony is very provisionally assigned. Alternatively, the specimen may be an immature *Tubulipora* or the encrusting base of an erect genus.



**Figs 2–3** *Stomatoporina* sp., NHM BZ 4766. **2**, entire colony with short lateral ramification arrowed, × 18. **3**, uniserial proximal branch, × 115.

### Family **TUBULIPORIDAE** Milne Edwards, 1838

### Genus ***IDMIDRONEA*** Canu, 1920

TYPE SPECIES. *Idmonea maxillaris* Lonsdale, 1845, by original designation (see Ostrovsky & Taylor 1996); Jacksonian (= Priabonian), Wilmington, North Carolina.

### **?*Idmidronea*** sp. Fig. 4

MATERIAL. NHM BZ 4768.

DESCRIPTION. Colony erect, branching, only proximal branches preserved, considerably thickened by kenozooidal overgrowths, basal branch up to 1.5 mm in diameter, attached to a cheilostome. Autozooids opening on laterofrontal sides of branches, with two or more apertures per series, most completely covered by kenozooidal overgrowths; visible apertures about 0.08–0.10 mm in diameter. Kenozooids extremely worn, narrow, apparently variable in growth direction.

REMARKS. This basal fragment of an erect colony is impossible to assign with certainty to a particular genus although the likelihood is that it belongs to the common and diverse genus *Idmidronea*. Hinds (1975) showed how homeomorphic genera of 'idmidroneid growth form' cyclostomes could be recognized on the grounds of the presence, orientation and skeletal organization of the kenozooids. Branches beyond the immediate vicinity of the colony base and in a good state of preservation are required before generic attribution can be undertaken using Hinds growth mode criteria. In the case of the Red Bluff Tuff specimen, it is impossible even to determine whether the overgrowing kenozooids are fixed-walled (i.e. having calcified exterior frontal walls) or are free-walled (i.e. lacking calcified exterior frontal walls).

### Family **CINCTIPORIDAE** Boardman, McKinney & Taylor, 1992

### Genus ***CINCTIPORA*** Hutton, 1873

TYPE SPECIES. *Cinctipora elegans* Hutton, 1873, by monotypy; Pliocene to Recent, New Zealand.

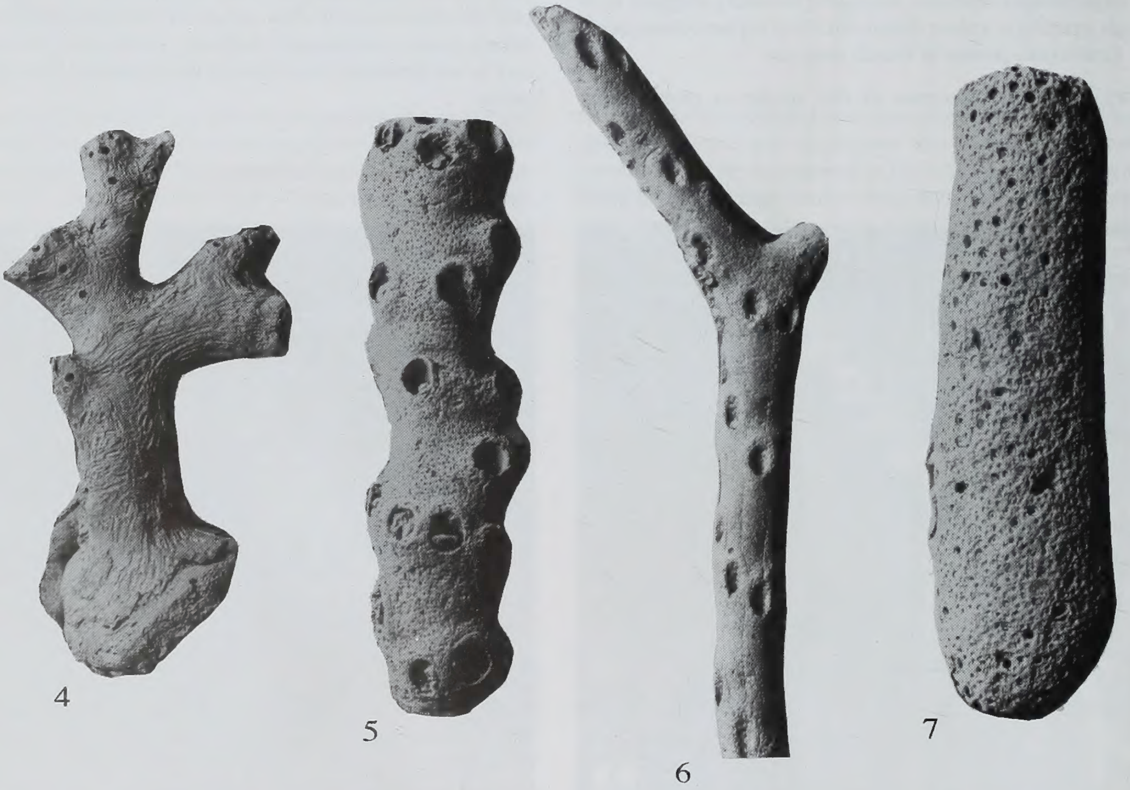
### ***Cinctipora solomoni*** sp. nov. Figs 8–11

HOLOTYPE. IGNS BZ 203–1, from Pukekio, Chatham Island.

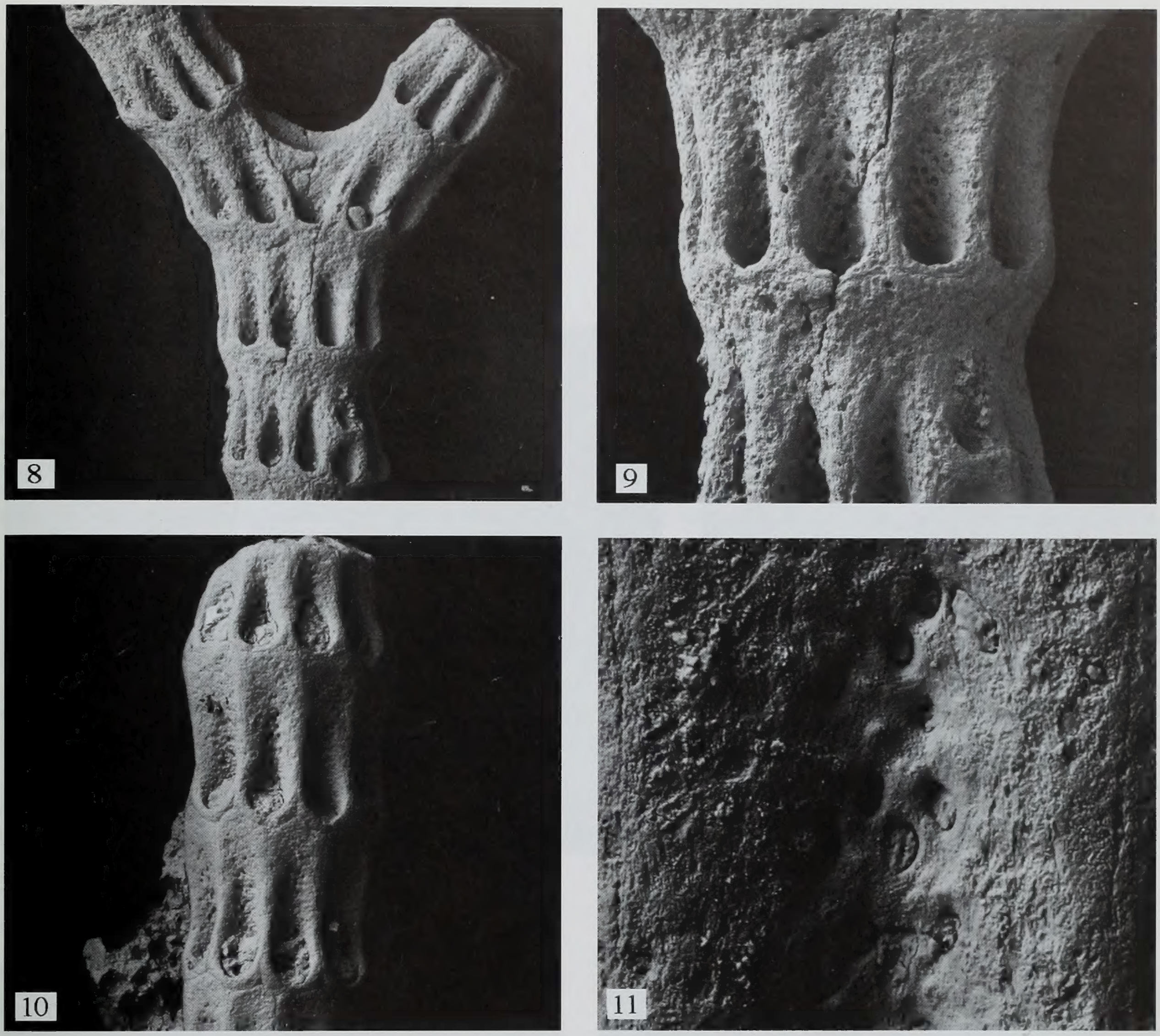
PARATYPES. IGNS BZ 203–2. NHM BZ 4769–4770.

NAME. To commemorate Tommy Solomon (Tame Horomona Rehe) who died in 1933 as the last full-blooded Moriori, the first people to inhabit the Chatham Islands.

DESCRIPTION. Colony erect, with narrow, cylindrical, bifurcating branches, 1.2–2.1 mm in diameter (typically less than 1.6 mm), widest immediately prior to bifurcation and narrowest immediately after bifurcation. Autozooids large, disposed in annular rings, 9–11 zooids around branch circumference. Skeletal organization free-walled, each autozooid intersecting colony surface at a low angle, with an elongate, subhexagonal skeletal shield averaging 1.18 mm in length (n = 23 zooids from 4 colonies; range = 0.98–1.37 mm) and 0.39 mm in minimum width (n = 23 zooids from 4 colonies; range = 0.30–0.54 mm). Skeletal shield having large interzooidal pores, diminishing in number distally, and occasional broad pustules.



**Figs 4–7** Erect branching cyclostomes. **4**, ?*Idmidronea* sp., NHM BZ 4768, proximal branches and colony base, × 11. **5**, ?*Attinopora* sp., NHM BZ 4771, × 29. **6**, 'Entalophorid' sp., NHM BZ 4773, bifurcating branch, × 12. **7**, ?*Tetrocycloecia* sp., NHM BZ 4778, worn branch, × 15.



**Figs 8–11** *Cinctipora solomoni* sp. nov. **8–9**, IGNS BZ 203–1, **holotype**; **8**, bifurcating branch, × 13; **9**, skeletal shields, including one example (lower right) divided by a transverse wall, × 40. **10–11**, IGNS BZ 203–2, **paratype**; **10**, × 28; **11**, interzooidal pores on skeletal shield, × 265.

Aperture width averages 0.23 mm (n = 23 zooids from 4 colonies; range = 0.18–0.30 mm).

REMARKS. This species is very similar to *C. elongata* Boardman *et al.* (1992) which is also recorded from the Chatham Islands, though from the considerably younger Whenuataru Tuff (Pliocene). However, colony branches in *C. solomoni* are typically narrower, with generally fewer zooids around the branch circumference (9–11 cf. 10–16), and the zooids are smaller and less elongate: length:minimum width ratio is about 3:1 in *C. solomoni* compared with 4:1 in *C. elongata*. Unlike other species of *Cinctipora*, none of the specimens of *C. solomoni* have terminal diaphragms but it is unclear whether this is due to preservational factors or ontogenetic stage of the available zooids, or is a species difference. Two autozooids from separate branches have a transverse wall subdividing their skeletal shields into proximal and distal halves (Fig. 9). In another branch the apertures of several proximal autozooids are plugged by clusters of small zooids which are best interpreted as kenozooids, although it is possible that they are the zooids of a fouling species which settled within the dead autozooids of an old branch of *C. solomoni*.

At the present day *Cinctipora* is endemic to the seas around New Zealand, and knowledge of the fossil record suggests that it has been so throughout the Neogene. Hitherto, the only pre-Neogene record of putative *Cinctipora* is from the Upper Cretaceous of South Africa (Boardman *et al.*, 1992), but there is some doubt about the correct attribution of this Upper Campanian or Maastrichtian species, especially in view of the small size of the zooids compared with all other cinctiporids which are characterized by zooidal gigantism. Therefore, the recognition of an unquestionable species of *Cinctipora* in the Red Bluff Tuff is important in providing a clear range extension of the genus in its modern biogeographical province back into the Late Paleocene or

Early Eocene. Unfortunately, the discovery of *C. solomoni* does not favour one or other of the two models for the origin of cinctiporids which were proposed by Boardman *et al.* (1992; note that a slight modification of model 1 has subsequently been presented as the preferred hypothesis by Boardman 1998).

### Genus *ATTINOPORA* Boardman, McKinney & Taylor, 1992

TYPE SPECIES. *Pustulopora zealandica* Mantell, 1850, by original designation; Recent, New Zealand.

**?*Attinopora*** sp. Fig. 5

MATERIAL. NHM BZ 4771–4772.

DESCRIPTION. Colony erect, with narrow, cylindrical branches, 0.7–0.9 mm in diameter, strongly curved in one specimen; bifurcations assumed to exist but not observed. Autozooids large, fixed-walled, frontal walls flat and minutely pseudoporous, about 0.9 mm long; zooidal boundaries not prominent; autozooids disposed in annular to irregularly spiral patterns with about 7 zooids around the branch circumference; apertures subcircular or slightly elongate longitudinally, 0.16–0.20 mm in diameter.

REMARKS. With only two small specimens available, it is impossible to be certain of the generic identity of this species. There are several genera of vinculariiform tubuliporines to which it may potentially belong, e.g., *Diaperoecia*, *Mecynoecia*, *Entalophoroecia*. However, the large size of the zooids and their arrangement on the colony surface, together with the biogeographical provenance, prompt a tentative identification as the cinctiporid genus *Attinopora*. Like other cinctiporids, gonozooids have never been observed in *Attinopora*, but a much larger suite of specimens would be needed for their absence to be reasonably established in the Red Bluff Tuff species.

### Family **ENTALOPHORIDAE** Auctt.

**'*Entalophorid*'** sp. Fig. 6

MATERIAL. NHM BZ 4773.

DESCRIPTION. Colony erect, with bifurcating cylindrical branches, slender, about 0.8 mm in diameter. Autozooids large, fixed-walled, 7–8 around the branch circumference; frontal walls slightly convex, slender, approximately 1.6–1.8 mm long by 0.4 mm wide, a narrow groove marking the zooidal boundary; apertures longitudinally elongate, 0.3 mm long by 0.2 mm wide. Gonozooids not observed.

REMARKS. The absence of a gonozooid in the solitary specimen belonging to this species precludes generic identification. In the older literature such vinculariiform tubuliporines are generally assigned to *Entalophora* Lamouroux, 1821 (type species *E. cellarioides* Lamouroux, 1821 from the Middle Jurassic). However, this genus is nowadays applied in a more restricted sense for species with simple, subtriangular gonozooids and, moreover, branches having a narrow axial canal (see Walter 1970). An axial canal is not present in the Red Bluff Tuff material.

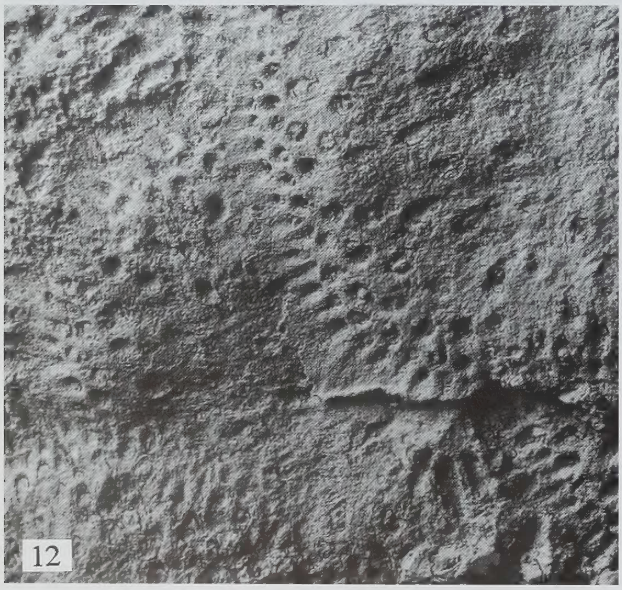
### Family **INCERTAE SEDIS**

### Genus '*BERENICEA*' Lamouroux, 1821

TYPE SPECIES. *Berenicea diluviana* Lamouroux, 1821, by subsequent designation; Jurassic (Bathonian), Calvados, France.

REMARKS. Following Taylor and Sequeiros (1982), the generic designation '*Berenicea*' is used informally for species of bereniciform tubuliporines in which the gonozooecium is unknown (*Berenicea* Lamouroux, 1821 is a *nomen dubium*).

12



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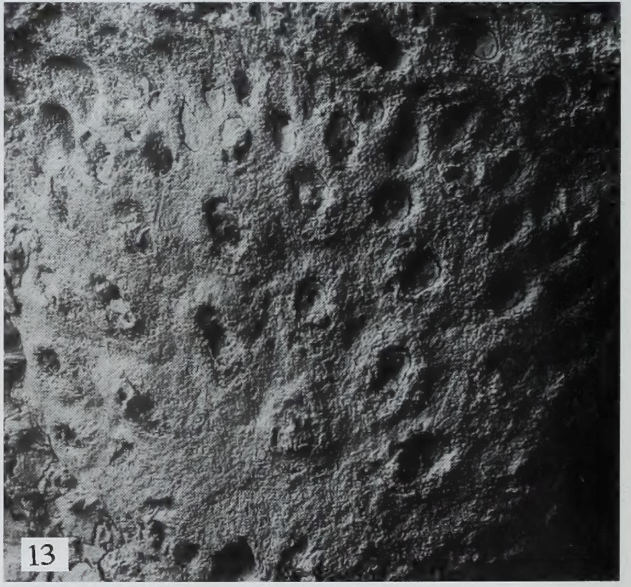


**Figs 12–13** '*Berenicea*' sp., NHM BZ 4774. **12**, ill-preserved, multilayered colony, × 37. **13**, lobate outgrowth, × 70.

### ***'Berenicea'* sp.** Figs 12, 13

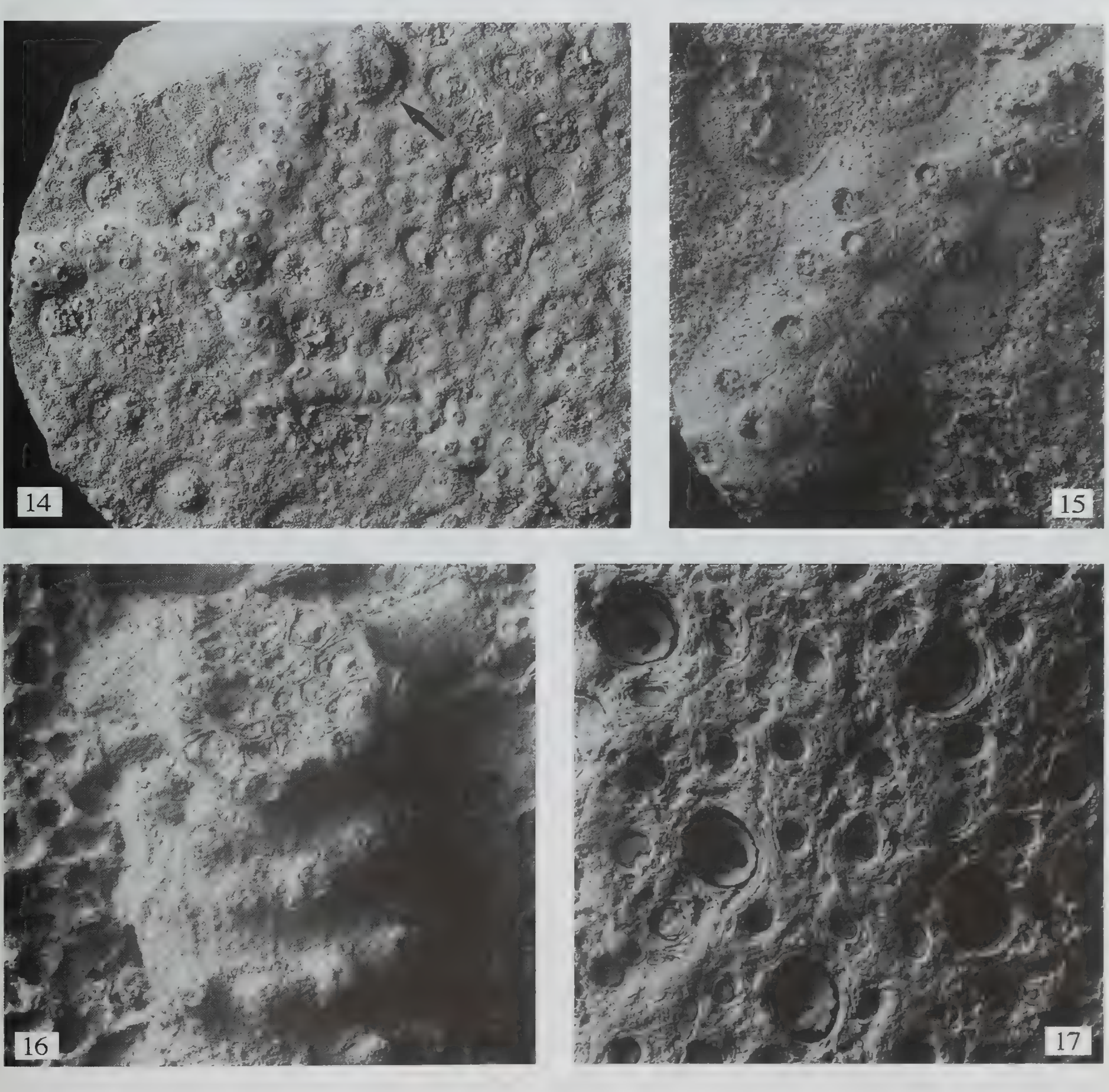
MATERIAL. NHM BZ 4774.

DESCRIPTION. Colony encrusting, multiserial, sheet-like, multilayered with superimposed discoidal subcolonies; maximum colony diameter 9 mm. Distal fringe of basal lamina broad, extending well beyond budding zone. Autozooids with gently convex frontal walls; apertures longitudinally elongate, about 0.15 mm long by 0.09 mm wide. Gonozooids not observed.

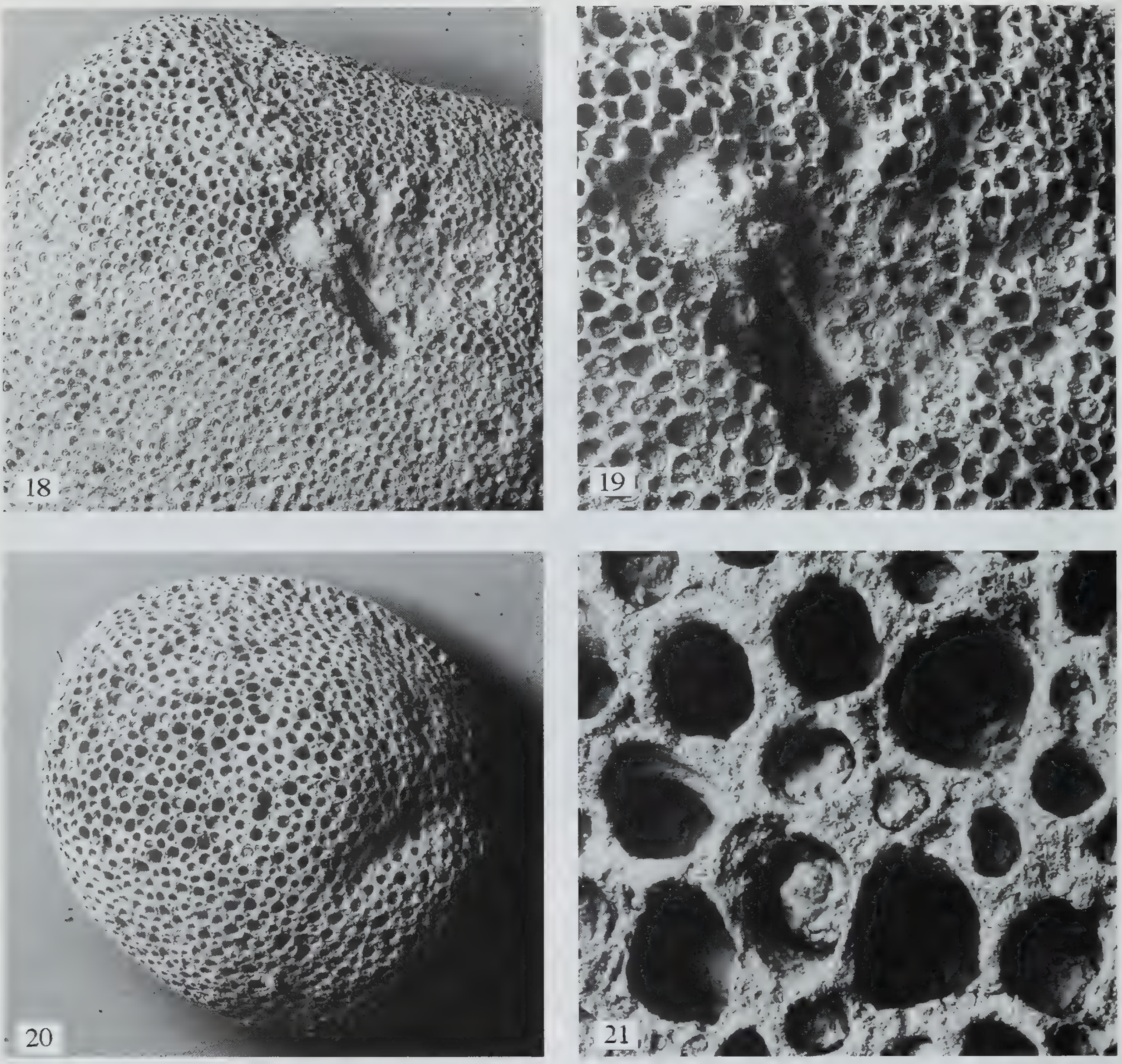
REMARKS. The only specimen is poorly-preserved, with a heavily corroded colony surface. In the absence of gonozooids the correct genus cannot be determined, nor can any useful comparisons be made with other species having the same general morphology. The multilamellar colony appears to result from eruptive budding of new subcolonies which grew as radial discs, covering the older zooids from previous layers, and prompting comparison with such species as *'Berenicea' sowerbyi* (Lonsdale) (see Pitt & Taylor 1990).

### Genus ***INCERTAE SEDIS***

REMARKS. The Red Bluff Tuff collection contains two examples of the encrusting basal parts of erect tubuliporine species. In both



**Figs 14–17** Miscellaneous cyclostomes. **14–15**, Erect tubuliporine base sp. 1, NHM BZ 4775; **14**, extensive, ramifying basal encrustation with broken stump of erect branch arrowed, × 13; **15**, autozooids flanked by kenozooids forming branch edges, × 54. **16**, Erect tubuliporine base sp. 2, NHM BZ 4776, encrusting zooids and stump of erect branch (top), × 52. **17**, ?*Tetrocycloecia* sp., NHM BZ 4778, detail of branch surface showing autozooidal and kenozooidal apertures with thick intervening walls, × 170.



**Figs 18–21** *Ceriopora rekohuensis* sp. nov. **18–19**, IGNS BZ 204–1, **holotype**; **18**, upper surface of colony, × 10; **19**, abraded gonozooid with roof remnant on left, × 35. **20–21**, NHM BZ 4777, **paratype**; **20**, entire colony, × 16; **21**, autozooidal and kenozooidal apertures, × 170.

cases only the broken stump of one erect branch remains, the arborescent parts of the colonies having been lost along with any taxon-diagnostic gonozooids. Characters of the basal zooids show quite clearly that the two specimens represent different species. However, it is unclear whether they are species whose erect branches have yet to be recovered in the Red Bluff Tuff, or if they are the bases of the three fixed-walled, erect species described above as ?*Idmidronea* sp., ?*Attinopora* sp. and 'Entalophorid' sp.

### ***Erect tubuliporine base*** sp. 1 Figs 14–15

MATERIAL. NHM BZ 4775.

DESCRIPTION. Colony base encrusting, comprising narrow (0.5–1.0 mm wide), oligoserial branches, with 2–4 series of autozooids bordered by kenozooids forming branch edges; branch profile low, gently convex; two branch bifurcations present, each at an angle of about 120°; stump of a broken erect branch, subcircular in cross-section, present at distal end of one of the encrusting branches. Autozooids with short, slightly convex frontal walls, about 0.4 mm long by 0.18 mm wide, their long axes divergent from branch mid-line; apertures more-or-less circular, 0.11–0.13 mm in diameter; pseudopores longitudinally elongate. Gonozooids absent.

REMARKS. The well-preserved colony, which encrusts an echinoid plate, has a maximum dimension of 7 mm and comprises three, long encrusting branches. The broken base of an erect branch is visible at the distal end of one of these three encrusting branches.

### ***Erect tubuliporine base*** sp. 2 Fig. 16

MATERIAL. NHM BZ 4776.

DESCRIPTION. Colony base encrusting, comprising a single oligoserial branch, about 1 mm wide, with 5–6 autozooidal series; branch profile high, well-rounded; stump of a broken erect branch, subcircular in cross-section, present at distal end of the encrusting branch. Autozooids with short frontal walls, about 0.5 mm long by 0.25 mm wide, attaining maximum width opposite the aperture; zooidal boundary walls slightly salient; apertures subcircular, small, 0.09–0.10 mm in diameter; pseudopores circular. Gonozooids absent.

REMARKS. This poorly-preserved specimen encrusts a pebble. Unlike the previous species, kenozooids do not appear to be developed at the edges of the branch, and the branch has a much more robust morphology.

## Suborder **CERIOPORINA** von Hagenow, 1851
## Family **HETEROPORIDAE** Waters, 1880

### Genus ***CERIOPORA*** Goldfuss, 1826

TYPE SPECIES. *Ceriopora micropora* Goldfuss, 1826, by subsequent designation of Gregory (1896); Upper Cretaceous, locality uncertain (see Nye 1976: 56).

REMARKS. The genus *Ceriopora* is here interpreted to include cerioporids with a semi-erect, 'massive' colony-form. Colonies tend to be globular, dome or mound-shaped, pedunculate or columnar. They lack the bushy morphology seen in other cerioporid genera (e.g. *Tetrocycloecia*, *Heteropora* auctt.) in which colonies are constructed of bifurcating cylindrical branches having a well-marked internal differentiation between endozone and exozone.

### ***Ceriopora rekohuensis*** sp. nov. Figs 18–25

HOLOTYPE. IGNS BZ 204–1, from Pukekio, Chatham Island.

PARATYPES. IGNS BZ 204–2 (thin sections plus remnants); NHM BZ 4777.

NAME. From Rekohu (Misty Skies), the Moriori name for Chatham Island.

DESCRIPTION. Colony small, the holotype measuring 8 mm in maximum width and the taller, sectioned paratype 10 mm high, pedunculate, a proximal stalk (broken-off in all available colonies) grading into an expanded head; head underside comprises exterior wall, upper surface covered by zooidal apertures of variable size, sometimes with larger autozooids distinct from smaller kenozooids but in other instances without obvious dimorphism in size; skeletal organization free-walled, apart from fixed-walled gonozooids. In thin section no clear distinction exists between endozone and exozone; budding apparently interzooecial in pattern; zooidal tubes long and gently curved in longitudinal section; walls variably moniliform, at least some of the constrictions marking positions of interzooidal pores, about 0.03–0.05 mm thick, not increasing appreciably in thickness from endozone to exozone; microstructure indistinctly laminated, cloudy, clotted in transverse sections of endozone; diaphragms present but extremely scarce; zooidal tubes disrupted by fouling organisms, including worm tubes, subsequently overgrown and embedded in colony structure. Autozooidal apertures subcircular, about 0.11–0.15 mm in diameter; kenozooidal apertures ovoidal, ranging down to 0.03 mm in diameter. Overgrown gonozooids visible in section (Fig. 25) and from one eroded example seen on surface of holotype; stellate in frontal outline, chamber extending as lobes between radial series of autozooidal apertures; floor formed of occluded, undifferentiated zooidal apertures; roof remnant probably comprising calcified exterior wall but microstructure poorly-preserved and no obvious pseudopores visible; ooeciopore not observed.

REMARKS. Most aspects of the morphology of this new species are very similar to the type species of *Ceriopora*, *C. micropora* Goldfuss, as redescribed by Nye (1976). These include the gently curved zooidal tubes with variably moniliform walls, and the indistinct dimorphism in zooidal aperture size. However, wall thickness and aperture diameter is slightly greater in the Red Bluff Tuff species. Whereas only questionable gonozooids in thin section were observed by Nye (1976) in *C. micropora*, the stellate frontal outline of the gonozooid in *C. rekohuensis* resembles that seen in *C. farringdonensis* Gregory (see Pitt & Taylor 1990: fig. 117D), an Aptian species in which dimorphism of zooidal aperture sizes is totally lacking. Judging from Cuffey & Sorrentino's (1985) redescription of three species of *Ceriopora* from the Pliocene of the eastern USA, all three species have zooids of distinctly larger diameter than *C. rekohuensis*.

### Genus ***TETROCYCLOECIA*** Canu, 1917

TYPE SPECIES. *Tetrocycloecia dichotoma* Canu, 1917, =*Ceriopora dichotoma* Goldfuss, 1827, *sensu* Reuss 1848, by original designation; Miocene, Eisenstadt, Austria (see Nye 1976: 147).

### ?***Tetrocycloecia*** sp. Figs 7, 17

MATERIAL. NHM BZ 4778–4780.

DESCRIPTION. Colony erect, with cylindrical, bifurcating branches, 1.3–2.1 mm in diameter; skeletal organization free-walled; colony surface with autozooidal apertures surrounded and separated by smaller, more numerous kenozooidal apertures; interzooidal walls very thick at colony surface. Autozooids long and horn-shaped in branch longitudinal sections, budded within an axial endozone; apertures small, 0.07–0.09 mm in diameter, elongated parallel to growth direction. Kenozooids seemingly budded closer to colony surface; apertures subcircular, 0.02–0.05 mm wide, typically less than half the diameter of neighbouring autozooidal apertures. Gonozooid unknown.

REMARKS. An etched, off-centred longitudinally ground surface provides the only indication of internal morphology in this species. In the absence of well-oriented thin sections, and of a gonozooid, this species can be no more than questionably assigned to *Tetrocycloecia*. Ranging from the Aptian to the Miocene (Pitt & Taylor 1990: 120), the relatively narrow branches of *Tetrocycloecia*, for example in *T. dichotoma* and *T. multiporosa*, with kenozooidal apertures considerably outnumbering autozooidal apertures, are, however, characters also seen in the Red Bluff Tuff species.

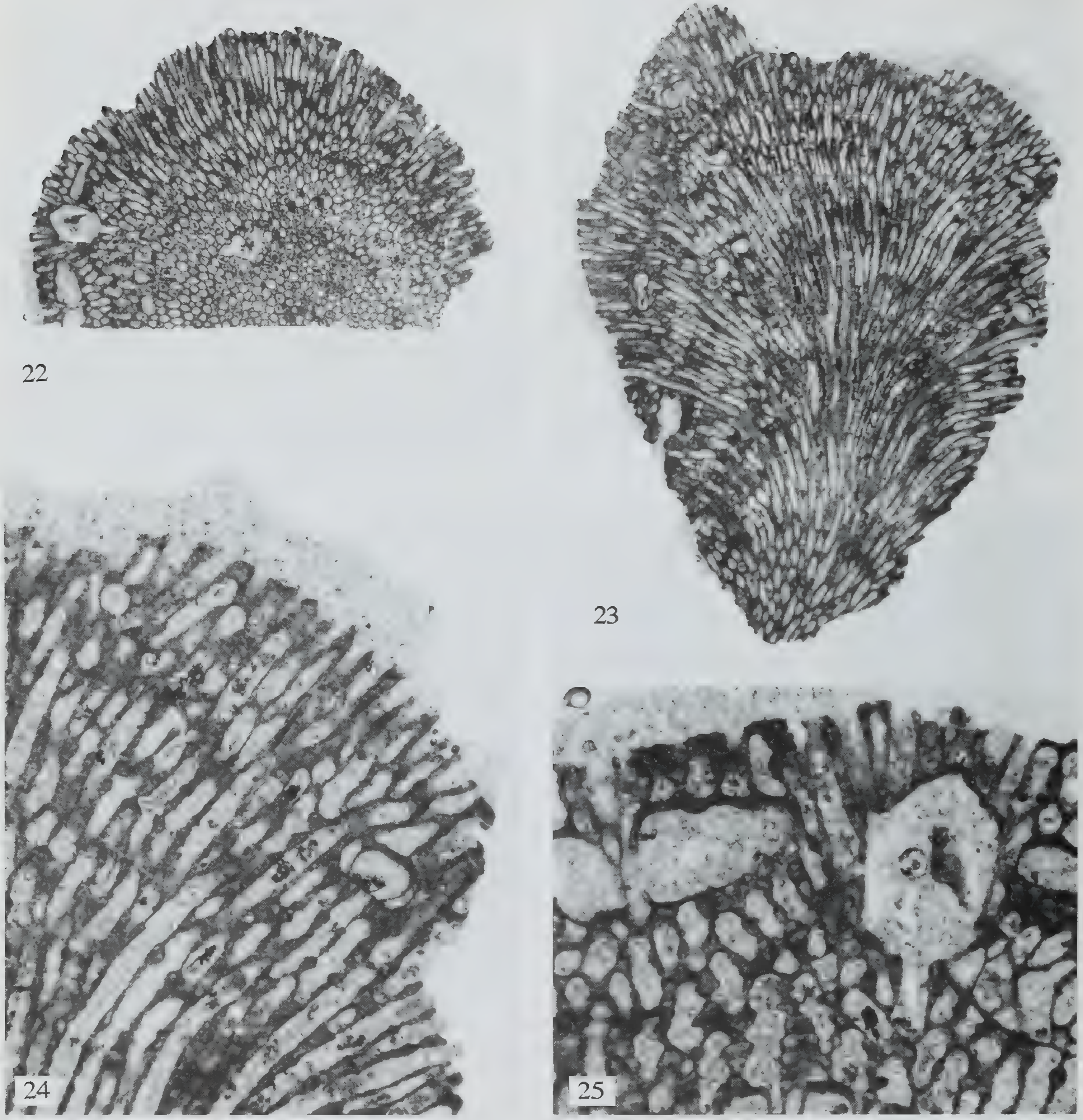
## Suborder **RECTANGULATA** Waters, 1887a
## Family **LICHENOPORIDAE** Smitt, 1867

### Genus ***DISPORELLA*** Gray, 1848

TYPE SPECIES. *Discopora hispida* Fleming, 1828, by original designation; Recent, Shetland Islands, U.K.

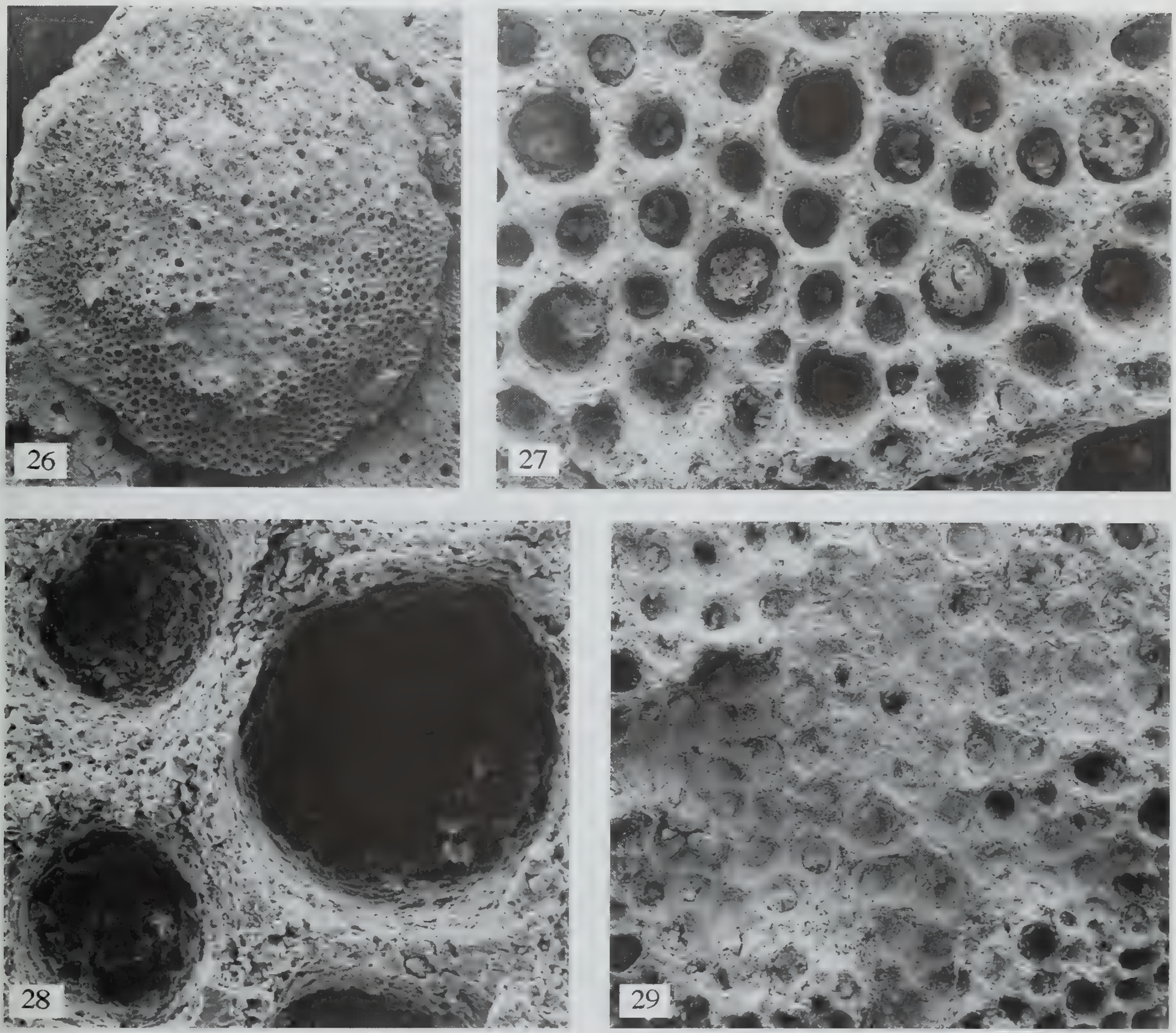
### ***Disporella*** sp. Figs 26–29

MATERIAL. IGNS BZ 205, a single colony encrusting the stylasterid *Sporadopora* cf. *marginata*, Pukekio, Chatham Island.



**Figs 22–25** *Ceriopora rekohuensis* sp. nov., thin sections, IGNS BZ 204–2. **22**, partial transverse section, × 9.5. **23**, oblique longitudinal section showing long, curved zooidal tubes × 10.5. **24**, detail of longitudinal section, × 33. **25**, overgrown gonozooids visible in the transverse section, × 33.

DESCRIPTION. Colony encrusting, more-or-less circular, maximum diameter 4.43 mm, maximum height 0.84 mm, completely adnate or the margin, slightly elevated above the substratum; marginal basal lamina little apparent, 0.35 mm wide where present; behind marginal lamina is a 0.75–1.31 mm wide zone of autozooids and kenozooids. Autozooids without projecting peristomes, and not aligned in definite radii, although up to 3–4 non-connate apertures may occur in a radial row amongst kenozooids; apertures 0.11 mm in diameter, the rim of even height all round. Kenozooid apertures 45–70% of the diameter of autozooidal peristomes, none closed by diaphragms. Brood chamber occupies most of colony centre, broken in the present colony; floor marked by thin layer of calcification over autozooids and kenozooids; almost none of the brood chamber roof remains except for a tiny area which indicates that thick-walled zooidal chambers may occur above the roof.



**Figs 26–29** *Disporella* sp., IGNS BZ 205. **26,** entire colony encrusting a stylasterid, × 14. **27,** edge of disk showing autozooidal and kenozooidal apertures, × 134. **28,** one autozooidal and two kenozooidal apertures, × 465. **29,** floor of brood chamber, with part of roof (?overgrown) present at upper left, × 29.

REMARKS. The loss of the brood chamber roof and the relative paucity of zooidal characters precludes naming this single specimen.

Class **GYMNOLAEMATA** Allman, 1856
Order **CTENOSTOMATA** Busk, 1852
Suborder **EUCTENOSTOMATA** Jebram, 1973
Family **IMMERGENTIIDAE** Silén, 1946

Genus ***IMMERGENTIA*** Silén, 1946

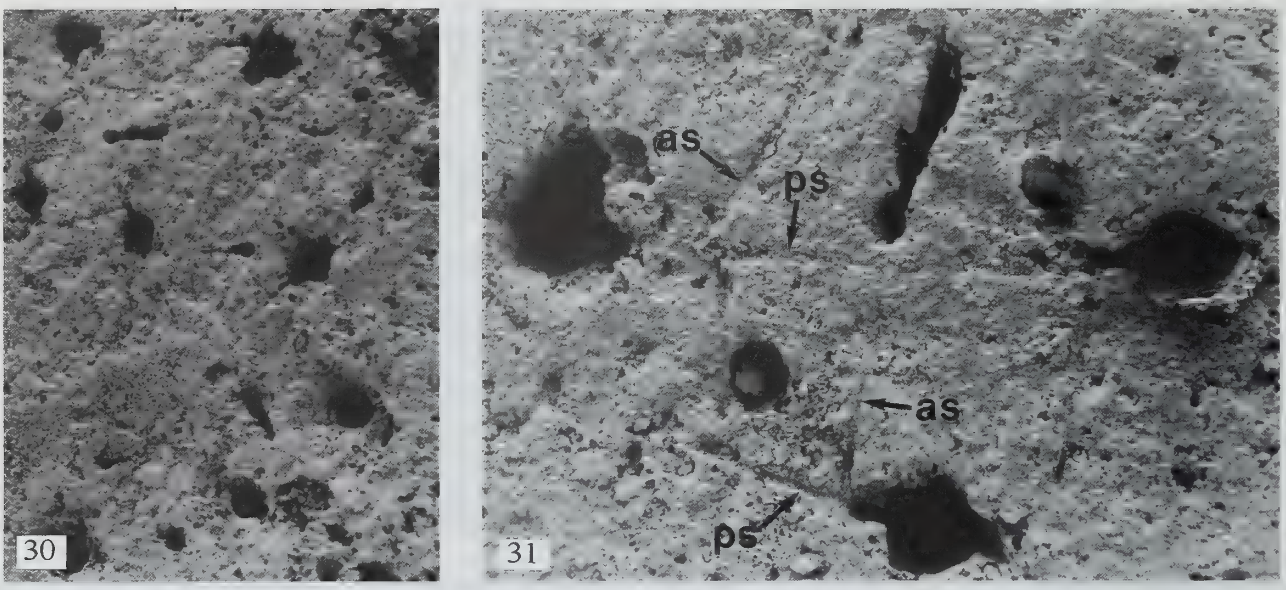
TYPE SPECIES. *Immergentia californica* Silén, 1946; original designation; Recent, California.

***Immergentia*** sp. Figs 30, 31

MATERIAL. IGNS BZ 206, a single colony fragment from Pukekio, Chatham Island.

DESCRIPTION. Colony boring in molluscan shell, the positions of zooidal orifices indicated by perforations in the shell surface. Perforations circular or, where the shell surface is slightly eroded, spindle-shaped, giving evidence of each zooid being connected directly to a principal stolon on each side of the ‘spindle’. Width of zooid at level of stolon connection 0.09 mm. Apparent distance between one zooid opening and the next connected by the same principal stolon 0.65 mm. Zooids vertical in the shell substratum, 0.52–0.58 mm long measured from the depth of the excavation. Principal stolons connected by adventitious (secondary) stolons that arise quite close to the zooidal aperture or at varying distances between consecutive apertures.

REMARKS. The monogeneric Immergentiidae is first recorded from the Santonian of Germany (Taylor 1993), subsequently becoming widely distributed in the Miocene of Europe, the USA, southeastern Australia, and New Zealand, and extending through the remainder



**Figs 30–31** *Immergentia* sp., NHM BZ 206. **30,** portion of surface of eroded molluscan shell with bryozoan borings, × 39. **31,** close-up of borings made by three autozooids; furrows indicating some of the traces of former principal stolons (ps) and adventitious stolons (as) are labelled, × 109.

of the Neogene to the present day. Three other boring ctenostome genera (Pohowsky 1978) have been accorded ranges coinciding with the age of the Red Bluff Tuff – these are *Orbignyopora* Pohowsky (?Silurian-Pliocene), *Penetrantia* Silén (?Lower Cretaceous-Recent), and *Spathipora* Fischer (nominally Jurassic-Recent, but the age and precise characters of the type species are uncertain). *Orbignyopora* can be discounted as a name for the Red Bluff Tuff specimen in that the zooids, although 'non-pedunculate' like *Immergentia* (i.e., separated from the principal stolon by a short connecting stolon), are disposed horizontally immediately beneath the shell surface. *Penetrantia* zooids are pedunculate, so this genus, otherwise common in the New Zealand Neogene, can also be ruled out. *Spathipora*, as understood, is also pedunculate and has never been recorded from the New Zealand region. No other genus of boring ctenostome accords with the characters of the form from Red Bluff Tuff and we are confident that the characters of the borings in the specimens correlate with the characters of *Immergentia*. We do not ascribe a species name to these borings, however, inasmuch as most of them are sediment-infilled, precluding polyester-resin casting which provides many more characters than are presently determinable.

### Order **CHEILOSTOMATA** Busk, 1852
### Suborder **FLUSTRINA** Smitt, 1868

REMARKS. Smitt's suborder included the families Flustridae, Cellariidae, and Membraniporidae (*sensu lato*, comprising later calloporids, chaperiids, etc.) but excluded many 'cellularine anascans' like *Aetea, Eucratea, Bugula,* etc. It is used here as an available taxon in a historically significant work (see Schopf & Bassett, 1973) in preference to Neocheilostomina d'Hondt (1985) which also included ascophorans.

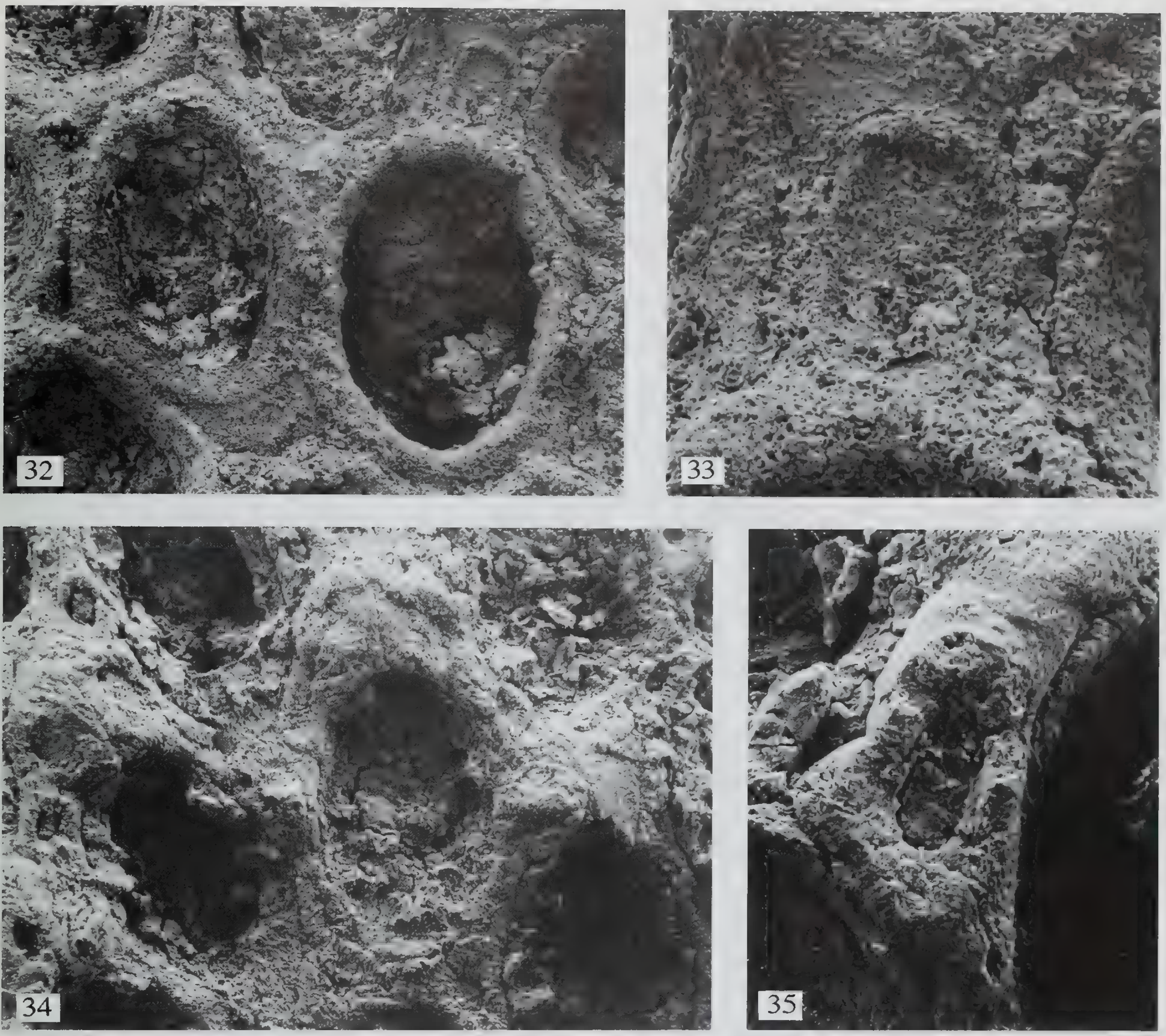
### Family **CALLOPORIDAE** Norman, 1903

### Genus ***FLUSTRELLARIA*** d'Orbigny, 1853

TYPE SPECIES. *Flustrellaria fragilis* d'Orbigny, 1853; by subsequent designation of Bassler (1935); Cenomanian, LeMans, France.

REMARKS. According to the taxonomic criteria used by d'Orbigny (1851–54), based on colonial and zooidal characters, *Flustrellaria* was established for membraniporiform unilaminate fragments whose zooids lacked frontal 'pores' (i.e., adventitious avicularia). The first-named species, selected as type by Bassler (1935), was *F. fragilis*, based on unattached fragments. According to the illustrations of this species (d'Orbigny 1853, pl. 723, figs 5–9) there is a large, rimmed opesia occupying most of the zooidal length, with a small to vestigial gymnocyst, and a dependent prominent hyperstomial ovicell apparently not closed by the zooidal operculum in life. Oral and marginal spine bases were not illustrated, but according to Canu (1900: 372) there are 8–10 spine bases in the specimen he examined from the d'Orbigny Collection, and spine bases are visible in photographs of the type and another specimen loaned by Prof. E. Voigt. A similar, shell-encrusting species, *Flustrellaria ornata* d'Orbigny, 1853 was illustrated with marginal spines (d'Orbigny 1853, pl. 728, figs 11, 12). This was chosen as the type species of *Ornatella* Canu, 1900, a new subgenus of *Membranipora* de Blainville. D'Orbigny's reliance on colonial characters, frequently superficial, was rejected by most late nineteenth- and early twenteeth-century bryozoologists including Canu, and *Flustrellaria* and related genera were relegated to *Membranipora*, ironically already a very heterogeneous taxon as then used. Accordingly, *Flustrellaria* has been scarcely used as a genus, although it was listed by Bassler (1935, 1953), who cited *Ornatella* as a junior subjective synonym.

It appears possible to use *Flustrellaria* as a valid genus, although SEM examination of d'Orbigny's material is desirable in order to



**Figs 32–35** Calloporid cheilostomes. **32–33**, *Flustrellaria australis* sp. nov., IGNS BZ 184, **holotype**; **32**, two entire autozooids, the one on the right with the base of a broken ovicell present on the gymnocyst of the distal zooid; note the lack of a proximal gymnocyst on some of the adjacent zooids, × 96; **33**, close-up of the broken ovicell base, × 287. **34–35**, *Akatopora chathamica* sp. nov., IGNS BZ 185–1, **holotype**; **34**, three ovicellate zooids, × 107; **35**, a heterozooid on the lateral rim of an autozooid, × 430.

give precision to the characters of the type species. One potential problem appeared in that d'Orbigny's family-rank taxon Flustrellaradae d'Orbigny, 1852 antedates the well-known equivalent taxon Calloporidae Norman, 1903. According to Sherborn (1899), however, the name Flustrellaradae was formally published in the year prior to its type genus, thus it may be treated as a *nomen nudum* and the current usage of family Calloporidae and superfamily Calloporoidea (Gordon 1989*a*) can remain unaffected.

An encrusting species from Chatham Island appears to conform to the characters of *Flustrellaria*, which, if the generic attribution is correct (the specimen appears to lack spine bases), would be the youngest species of the genus, extending the range beyond the KT boundary.

### *Flustrellaria australis* sp. nov. Figs 32, 33

HOLOTYPE. IGNS BZ 184, from Pukekio, Chatham Island. No paratypes.

NAME. From the Latin, *australis*, southern.

DESCRIPTION. Unique colony encrusting, unilaminate; multiserial but somewhat linear in form with maximum diameter 14 mm (ca. 10 mm on one side of the ancestrular region) but, since the substratum is fractured, the original diameter may have been several mm longer; with pluriserial lobes 2–?8 zooids wide. Zooids arranged quincuncially, each being surrounded by 6 others, suboval to pyriform in shape; length = 0.29–0.39 mm, width = 0.28–0.30 mm in the zone of astogenetic change; length = 0.44–0.62 mm, width = 0.31–

0.47 mm in the zone of astogenetic repetition. Zooidal margin somewhat thick-rimmed; the presence of marginal spine bases in the present material equivocal owing to inadequate preservation. Proximal gymnocyst absent to infrequently present, occupying up to 20% of zooidal length, with the proximal ends of the lateral rim encroaching onto it; or the gymnocystal area slightly depressed, with the faint outline of the base of a broken ovicell on it. Avicularia not present. Complete ovicells absent, but the base of one broken ovicell (Fig. 33) clearly indicates a disproportionately small, dependent hyperstomial ovicell not closed by the zooidal operculum in life. Ancestrula unknown, the ancestrular region missing.

REMARKS. Better-preserved material is needed to determine if oral and marginal spines are truly lacking, and complete ovicells would give precise evidence of the relationship of the ovicell opening to the maternal zooid.

This is a rare species. The sole colony encrusts a stylasterid (*Sporadopora* cf. *marginata* Tenison-Woods).

### Genus ***AKATOPORA*** Davis, 1934

TYPE SPECIES. *Akatopora clausentina* Davis, 1934, by monotypy; Lutetian, Southampton, England.

### ***Akatopora chathamica*** sp. nov. Figs 34, 35

HOLOTYPE. IGNS BZ 185–1, from Pukekio Hill, Chatham Island.

PARATYPES. IGNS BZ 185–2; NHM BZ 4781.

NAME. From the name of the main island in the Chathams group.

DESCRIPTION. Colony encrusting, unilaminate, multiserial, with maximum diameter 13 mm. Zooids arranged quincuncially, more or less elongate-oval in shape; length = 0.41–0.49 mm, width = 0.24–0.28 mm in the zone of astogenetic repetition. Zooidal opesia oval, bordered on each side by a narrow lateral cryptocyst, probably originally granular, broadening to a sloping shelf proximally. Boundaries between zooids concealed by contiguous adventitious avicularia or kenozooids that occur along the rims; these heterozooids variable in shape, generally elongate on the lateral rims in the direction of zooid growth, or more subquadrangular to subtriangular at the proximal corners of the zooid where they are paired and partly cover the cryptocyst; the frontal chamber walls elongated along the margins so that adjacent polymorphs are continuous. Heterozooid opesia oval; a cross-bar or distinct condylar pivots not evident. Ovicell hyperstomial, though somewhat recumbent on the proximal part of the cryptocyst of the succeeding zooid; the ectooecial surface smooth with a thin median suture line; becoming covered on both sides of the suture line by secondary calcification that may represent kenozooidal overgrowth. Ovicell probably closed by the zooidal operculum in life. Ancestrula unknown, the ancestrular region missing.

REMARKS. Preservation is generally poor but, because of the occurrence of ovicells and adventitious heterozooids, is adequate to show the distinctive characters of the genus and species. *Akatopora* was first described monotypically by Davis (1934) who interpreted the chambers of the interzooidal polymorphs as 'lacunae' in 'interoecial secondary tissue', applying the terminology used by Lang (1916, 1921) for cribrimorph cheilostomes. Because of their variable size he concluded that the lacunae could not be avicularia. Subsequently, Gordon (1986) recognised Pleistocene-Recent *Aplousina* (?) *circumsaepta* Uttley, 1951 from New Zealand as congeneric with *Akatopora*. Study of fresh specimens (deep purple in life) and scanning electron micrographs make it clear that these variable-sized chambers are heterozooids comprising both avicularia and kenozooids. The avicularia are distinctly differentiated into a rostral area and opesia with proximal cryptocyst, whereas kenozooidal opesiae are entirely surrounded by a narrow granular cryptocyst (see Taylor *et al.*, 1989, fig. 9A). The ovicells of *A. circumsaepta* become covered over by thin kenozooidal chambers, and this appears to be the case in *A. chathamica*.

*Akatopora circumsaepta* has a much narrower proximal zooidal cryptocyst and lacks an ectooecial median suture, otherwise the two species are very similar. Additionally, *A. circumsaepta* has an obligate symbiotic relationship with hermit crabs in bryozoan-modified gastropod-shell extensions (Taylor *et al.*, 1989; Taylor 1994), whereas *A. chathamica* (two specimens) encrusted what appears to have been dead (disarticulated and broken) bivalve shell. No other fossil *Akatopora* species is known in the New Zealand region and *A. chathamica* is the earliest record of the genus globally.

## Family **CALESCHARIDAE** Cook & Bock, in press

### Genus ***CALESCHARA*** MacGillivray, 1880

TYPE SPECIES. *Eschara denticulata* MacGillivray, 1869, original designation; Recent, SE Australia.

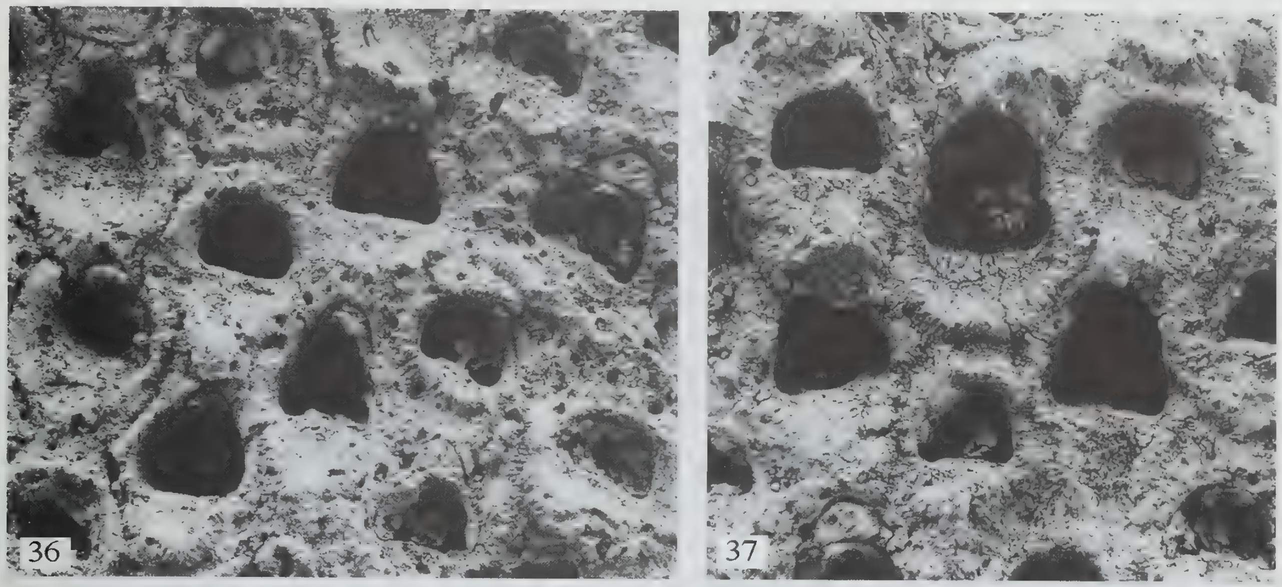
### ***Caleschara*** sp. Figs 36, 37

MATERIAL. IGNS BZ 207, a single colony from Pukekio, Chatham Island.

DESCRIPTION. Colony of unique specimen encrusting, in places multilamellar owing to self-overgrowth. Zooids large, dimorphic, arranged quincuncially, length = 0.65–0.97 mm, width = 0.52–0.71 mm, with distinct interzooidal grooves. The cryptocystal shelf slopes inward from the proximal rim where it is highest to the mostly horizontal edge of the opesia where it appears to descend abruptly toward the zooidal interior; opesiae variable in shape depending on overall shape of zooid, ranging from a normally high-arched D shape to roundly triangular, widest proximally where it is 0.28–0.46 mm wide. Brooding zooids larger than autozooids overall, although some dimensions may overlap; 0.89–1.03 mm long including ovicell, 0.69–0.74 mm wide; easily distinguished not only by size but more especially by the distal ovicell chamber, which is not concealed by cryptocyst in the present material but, owing to poor preservation, it is not possible to say if this is because of breakage and loss of a cryptocystal cover; because there is no cryptocyst cover the opesiae appears very long; width of brooding zooids 0.46–0.50 mm. Avicularia not seen.

REMARKS. Thanks to a recent revision of the genus *Caleschara* and a better appreciation of its characters (Cook & Bock, in press) it is now possible to compare the present material with the known living and fossil species. Recent *Caleschara* is mostly Indo-West Pacific in distribution, and fossil species are predominantly Australian with the exception of the oldest-known species of the genus, *C. squamosa* Meunier & Pergens, from the Danian of Belgium. The present material thus constitutes the earliest occurrence of the genus in the Australasian region.

Although preservation of the Red Bluff Tuff specimen is poor, the generic attribution appears reliable. Owing to the imperfect expression of the characters of the brooding zooids, however, we prefer not to erect a new species name until better-preserved material is found. Pitting of the skeletal surface is pervasive and even gives the impression of holes where oral-spine bases might occur. This is



**Figs 36–37** *Caleschara* sp., IGNS BZ 207. **36,** autozooids with variably-shaped opesiae, × 33. **37,** opesiae and cryptocysts, × 60.

almost certainly an artifact, especially since oral spines are not known in any other species of Calescharidae. The Red Bluff Tuff specimen most closely resembles the morphology expressed in some populations of Recent *C. minuta* Maplestone which lack a median process of the cryptocyst. Lack of this process is more typical of the calescharid genus *Tretosina* Canu & Bassler, 1927 which typically has longitudinally elongate-oval opesiae, unlike those in *Caleschara* and the present specimen.

### Family **MICROPORIDAE** Gray, 1848

### Genus ***MICROPORA*** Gray, 1848

TYPE SPECIES. *Flustra coriacea* Johnston, 1847, *non* Esper, 1796, by monotypy; Recent, NE Atlantic.

### ***Micropora quadriporosa*** sp. nov. Figs 38, 39

HOLOTYPE. IGNS BZ 186, from Pukekio, Chatham Island. No paratypes.

NAME. Alluding to the number of opesiular pores (four) in the zooidal cryptocyst.

DESCRIPTION. Colony encrusting, tiny, apparently with very short pluriserial groupings of zooids. Zooids oval to subpyriform, mostly contiguous, but some very slightly disjunct and thus separated by distinct interzooidal furrows; length = 0.33–0.45 mm, width = 0.24–0.28 mm. Zooids generally with smooth, steeply sloping gymnocystal sides and sometimes a short proximal gymnocyst, accentuating the appearance of a raised cryptocystal rim. Cryptocyst at a lower level than the rim, more or less flat and granular, with 4 circular opesiules; one on each side proximal to the orifice, the other pair near the proximal end of the cryptocyst. Orifice more or less semicircular, but nearly twice as wide as long. No oral spines. Avicularia interzooidal, the combined rostral-opesial area somewhat pyriform in shape, indented in the middle on each side, possibly lacking a complete cross-bar. Ovicell present (broken in the only specimen), hyperstomial, evidently not closed by the zooidal operculum in life, the outer skeletal surface apparently smooth and imperforate when fresh. Basal pore-chambers present in distal half of zooids.

REMARKS. In its range of characters, the genus *Micropora* is quite variable. Species generally have a deep pair of recessed suboral opesiules but a few have two to many accessory opesiules (e.g., *M. variperforata* Waters, 1887b; *M. gracilis* (Uttley, 1949)); most lack oral spines, but a few species have them (e.g., *Micropora stenostoma* (Busk, 1854); *M. notialis* Hayward & Ryland, 1993); avicularia are generally present, but are lacking in some species (e.g., *M. coriacea* (Johnston, 1847); *M. inarmata* Soule, 1959); ovicells are characteristically imperforate, but *M. santacruzana* Soule, Soule & Chaney, 1995 is pseudoporous; how the genus may be split, if this is appropriate, is uncertain, although d'Hondt & Gordon (1999) have segregated as a new genus (*Promicroa*) a strictly biserial form with pseudoporous ovicells and erect dichotomous branches. Because of occlusion of avicularian opesiae in the present material it is uncertain whether *M. quadrispinosa* lacks complete cross-bars. If they are lacking, this character, the tendency to disjunct zooids separated by deep furrows, and especially the hyperstomial ovicell not closed by the zooidal operculum, may warrant future segregation at the generic level.

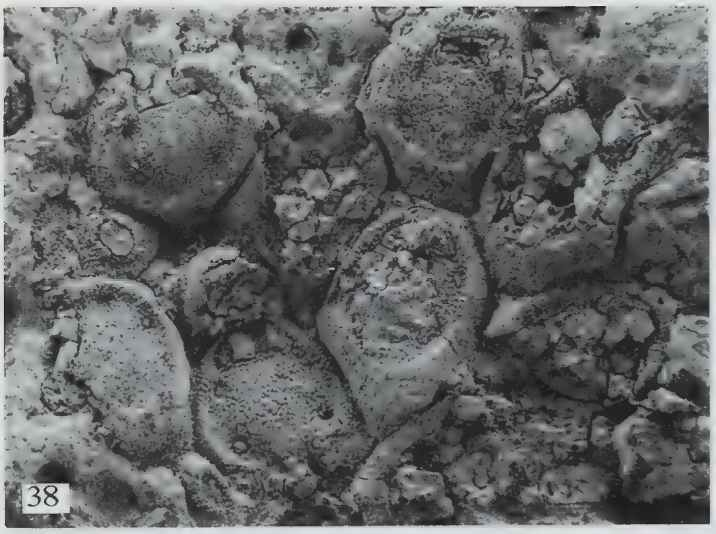
### Genus ***HOPLITAECHMELLA*** Voigt, 1949

TYPE SPECIES. *Cellepora vespertilio* von Hagenow, 1839, by original designation; Upper Senonian, Rügen, Germany.

### **?*Hoplitaechmella*** sp. Figs 40–42

MATERIAL. IGNS BZ 208, a single colony fragment from Pukekio, Chatham Island.

DESCRIPTION. Colony encrusting. Autozooids arranged quincuncially; length = 0.52–0.60 mm, width = 0.43–0.45 mm. Cryptocyst granular (preservation of granulation seen proximal to the orifice in one zooid). Opesia-orifice wider (0.20–0.24 mm) than long, the proximal rim gently concave, with distinct rounded opesiular indentations at the corners. Oral-spine bases not apparent. As many as three small avicularia occur along each lateral margin interzooidally,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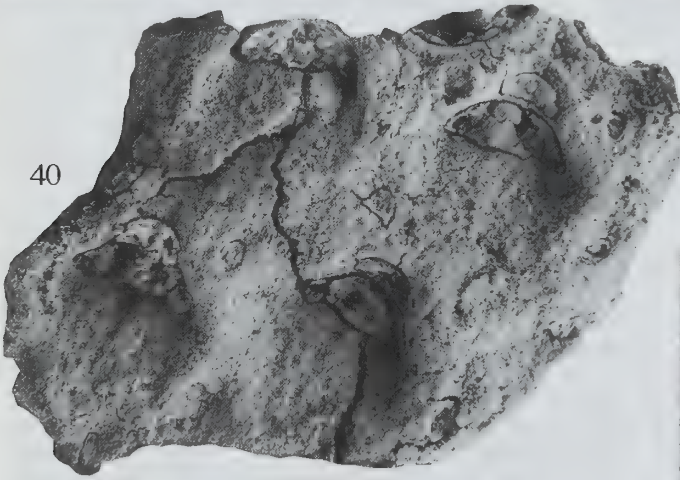
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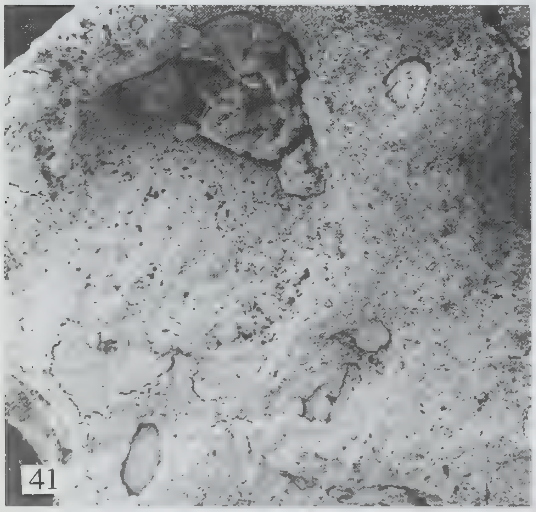
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**Figs 38–42** Microporid cheilostomes. **38–39**, *Micropora quadriporosa* sp. nov., IGNS BZ 186, **holotype**; **38,** part of a small colony, one zooid ovicelled and two interzooidal avicularia seen at left, × 65. **39,** ovicelled zooid seen in 38, with an interzooidal avicularium at lower left, × 152. **40–42** ?*Hoplitaechmella* sp., IGNS BZ 208; **40,** colony fragment with ovicelled zooids, × 60; **41–42,** close-up of zooids in Fig. 40; note occluded openings of ovicells and probable avicularia interzooidally, × 115 and × 130 respectively.

obscuring interzooidal boundaries; in the poorly-preserved material at hand these appear to be elongate-oval, with a single central foramen surrounded by a concentric granular cryptocyst. Ovicell endozooidal, immersed under the succeeding cryptocyst, the more-or-less semicircular opening occurring immediately distal to the opesia-orifice.

REMARKS. The single tiny specimen, imperfectly preserved, comprises only three complete zooids, all fertile, with parts of adjacent broken zooids. Most of the diagnostic characters are present but the generic attribution is uncertain. *Aechmella* Canu & Bassler, 1917 seems ruled out, as the interzooidal avicularia of the type species are relatively large and distinct with acute rostra *Hoplitaechmella* species have numerous small avicularia, occasional vicarious avicularia, and endozooidal ovicells as in the present material but distinct oral-spine bases occur in the type and other species (see Voigt 1949; Berthelsen 1962).

Known species include:

*H. antecedens* (Brydone, 1914), Upper Senonian, England
*H. deshayesi* (von Hagenow, 1851), Upper Senonian, The Netherlands
*H. nitescens* (Brydone, 1914), Upper Senonian, England
*H. nonna* (von Hagenow, 1839), Upper Senonian, Germany
*H. smitti* (Hennig, 1892), Danian, Sweden and Denmark
*H. vespertilio* (von Hagenow, 1839), Upper Senonian, Germany
*H. vespertilioides* Berthelsen, 1962, Upper Danian, Denmark.

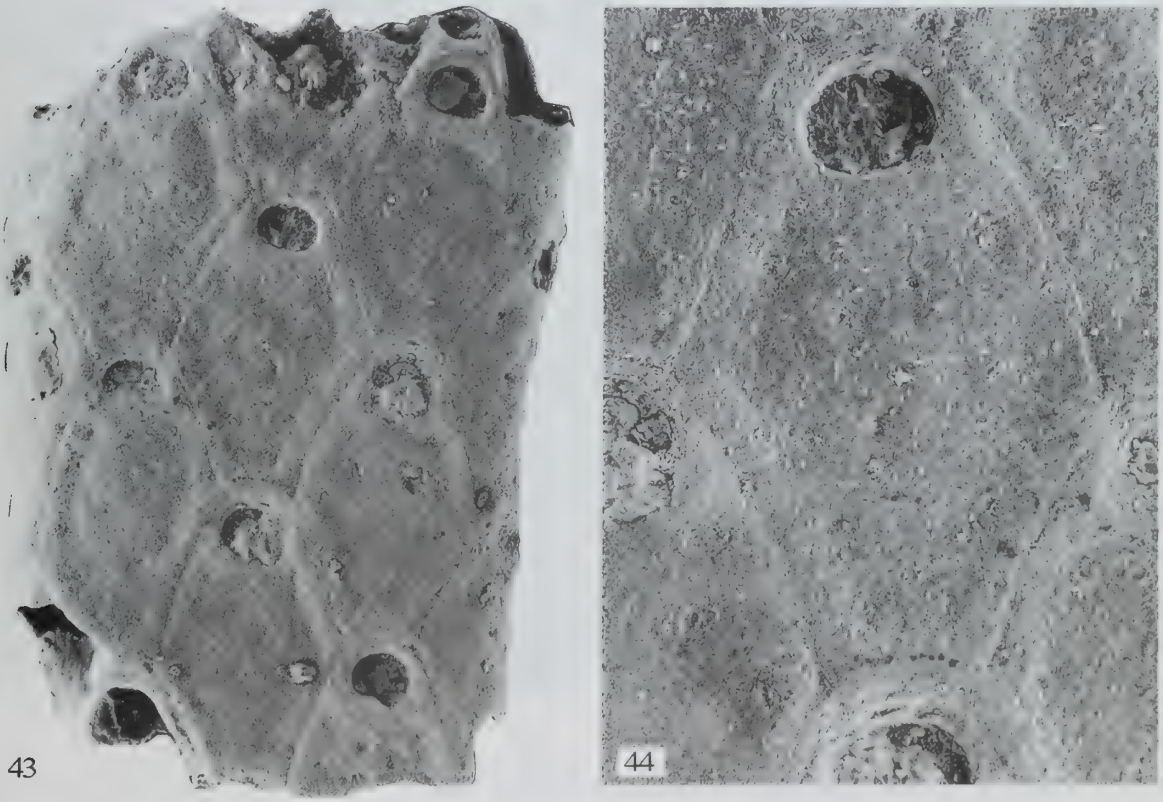
If the present material is *Hoplitaechmella*, then it represents the first known occurrence of the genus outside Europe, and the youngest stratigraphical record.

### **Microporid** sp. Figs 43, 44

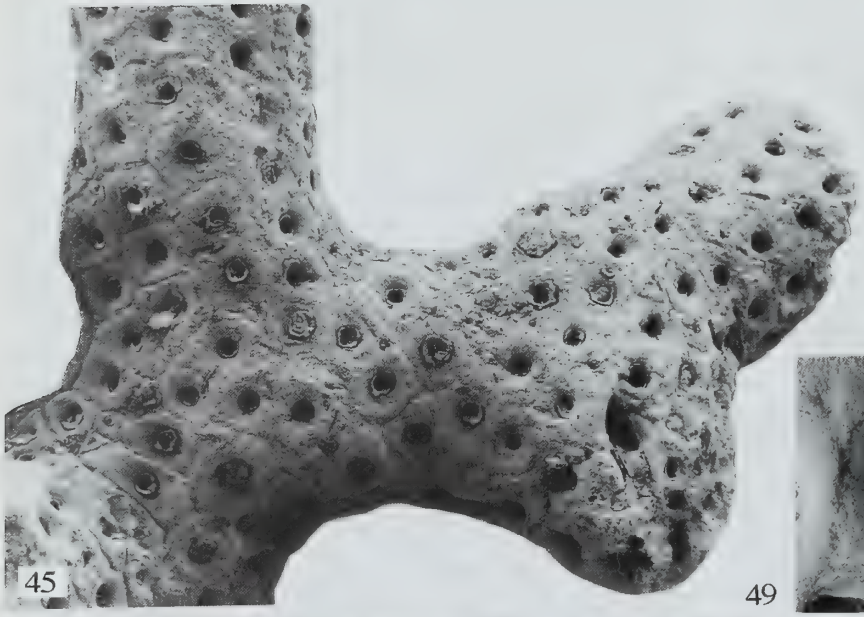
MATERIAL. IGNS BZ 209, a unique specimen from Pukekio, Chatham Island.

DESCRIPTION. Specimen erect, apparently slightly worn, comprising part of a narrow bilamellar branch, 1.75 mm long and up to 1.16 mm wide. Zooids sub-elongate, widest in the middle, tapering distally and proximally, length = 0.62–0.69 mm, width = 0.41–0.45 mm, arranged such that there are three alternating longitudinal rows facing frontally on each side of the branch, separated by a row along each branch margin that faces laterally. Zooidal frontal shields flattened with the rims slightly elevated above the shield centre, implying a cryptocyst. Faint paired excavations proximolateral to the orifice in several zooids indicate opesiules; additional faint excavations may occur along the margins and in the centre of the shields, indicating possible accessory opesiules as well as sparse pseudopores. Opesia/orifice generally transversely oval, wider (0.13–0.15 mm) than long (0.10–0.11 mm). Oral spine bases absent, with the possible exception of one orifice in which a faint pair of excavations occurs distally. Ovicells and avicularia not present in the sole fragment.

REMARKS. Owing to the paucity of diagnostic characters it is not possible to be certain of the genus. Maastrichtian *Puncturiella* Levinsen (type species *P. gudumensis* Levinsen, 1925) is characterised by cylindrical stems of zooids with coarsely perforated frontal shields and dimorphic opesiae/orifices. Species of the nominal subgenus *Puncturiellina* Voigt (type species *Puncturiella* (*Puncturiellina*) *subsculpta* Voigt, 1987) (Maastrichtian-Danian) exhibit a range of colony forms including erect-bilamellar, the frontal



**Figs 43–44** Microporid sp., IGNS BZ 209. **43,** part of erect bilamellar colony fragment, × 59. **44,** close-up of an autozooid; positions of possible suboral opesiules and frontal pseudopores faintly indicated, × 126.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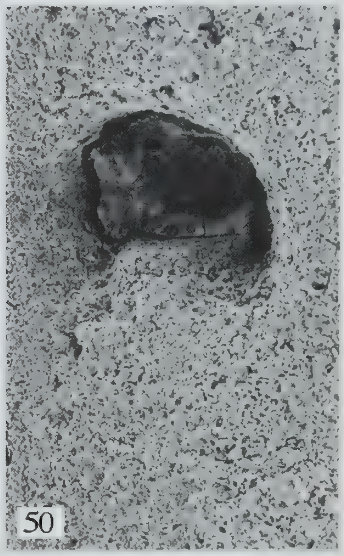
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**Figs 45–50** Onychocellid cheilostomes. **45–47,** *Inversaria gondwanae* sp. nov.; **45,** IGNS BZ 187–1, **holotype**, erect branching colony, × 14; **46,** IGNS BZ 187–2, autozooids and orifices; note the granulation of the cryptocyst in one zooid and circular holes indicating the location of possible heterozooids in some zooids, × 65; **47,** IGNS BZ 187–3, longitudinal section of a branch showing interiors of two peristomes and parts of two autozooids, × 116. **48–50,** *Chondriovelum fossilis* sp. nov.; **48,** IGNS BZ 188–2, part of a branch, proximally fractured, × 38; **49,** IGNS BZ 188–1, **holotype**, vicarious avicularium, × 67; **50,** IGNS BZ 188–3, autozooidal orifice, × 180.

shields are less coarsely perforated, and opesiae/orifices are monomorphic and semicircular. Ovicells are lacking and, although characteristic small avicularia occur distally to the orifices, they do not occur on every zooid. Lutetian-Bartonian *Poropeltarion* Cheetham (type species *P. lebanonense* Cheetham, 1963) has frondose to narrow-branched bilamellar colonies of pseudoporous zooids. Both avicularia and ovicells are lacking. Recent *Promicroa* d'Hondt & Gordon, 1998 from the Norfolk and Kermadec Ridges in the Southwest Pacific produces erect, narrow-branched colonies, but these are unilamellar and the zooids have both semicircular orifices and ovicells; there are no avicularia. In the sum of the limited number of characters available, the Chatham Island specimen most closely resembles species of *Poropeltarion*, or possibly *Puncturiellina*.

### Family **ONYCHOCELLIDAE** Jullien, 1882

### Genus ***INVERSARIA*** von Hagenow, 1851

TYPE SPECIES. *Ceriopora tubiporacea* Goldfuss, 1826, subsequent designation by Gregory, 1899; Upper Maastrichtian, Maastricht, The Netherlands.

***Inversaria gondwanae*** sp. nov. Figs 45–47

HOLOTYPE. IGNS BZ 187–1, from Pukekio Hill, Chatham Island.

PARATYPES. IGNS BZ 187–2, 3. NHM BZ 4782, 4783 (sample).

NAME. Alluding to the first record of the genus in a part of former Gondwana.

DESCRIPTION. Colony erect, stout, irregularly branching, attached by a somewhat thickened base not greater than 4 mm in maximum width or diameter. Wide-angled bifurcations are usual but, as at a rare anastomosis of branches in a colony, 3–4 branches may originate; each branch pair of a bifurcation is in the same plane but other bifurcations are in other planes. Branches more or less cylindrical, ranging (among the broken fragments available) from 0.74–3.27 mm diameter, widening to ca. 4.5 mm before the widest bifurcation. Autozooids in 9–11 regularly alternating longitudinal series, increasing to 20 such series immediately proximal to a bifurcation; zooid outlines defined by shallow interzooidal grooves, diamond-shaped with four sides and widest at the lateral points or the distal and proximal and/or lateral points truncated so that the shape is unevenly 6–8 sided; often wider (0.46–0.63 mm across the width of the diamond) than long (0.37–0.58 mm). Zooidal cryptocyst evenly granular in the best-preserved example, sloping, initially shallowly then steeply, all around the opesia which is more distally placed, with a straighter proximal rim, in neanic zooids and centrally placed and circular in ephebic zooids with thicker frontal calcification. Opesial-peristomial shaft of equal longitudinal diameter, sloping inwards proximally and widening from 0.15 mm at the level of the primary orifice to 0.20 mm at the frontal opening. Simple avicularium-like heterozooids may occur between zooids in a longitudinal series (i.e., between the lateral points of adjacent zooids in transverse rows); more or less circular or transversely oval with a small concentric foramen. Ovicells not seen frontally or in section.

REMARKS. *Inversaria* is a relatively little-known genus, originally attributed to the Cyclostomata. Voigt and Williams (1973) reviewed the known species, described them, and gave stratigraphic ranges and geographic distributions as follows:

*I. tubiporacea* (Goldfuss, 1826), Campanian-Maastrichtian, ?Danian, The Netherlands, Belgium, Germany.

*I. crassipes* (Marsson, 1887), Lower Maastrichtian, Germany, Denmark, Poland.

*I. flabellula* (von Hagenow, 1846), Upper Campanian, Sweden.

*I. ramosissima* (Eichwald, 1865), Upper Maastrichtian, Lower Danian, Crimea, Ukraine.

*I. trigonopora* von Hagenow, 1851, Upper Maastrichtian, Belgium, The Netherlands.

*I. tuber* Voigt & Williams, 1973, Upper Maastrichtian, The Netherlands.

*I. verrucosa* Voigt, 1962, Upper Maastrichtian, Crimea, Ukraine.

Colonial morphology among these species ranges from mounded, through erect and branching to bilamellar-foliaceous. Cryptocystal morphology is relatively similar throughout the species, which all have deep peristomial shafts. Calcified opercula and occlusor muscle scars have been preserved in some material of the type species (Voigt & Williams 1973). The present species most closely resembles *I. crassipes* in colonial and zooidal morphology, but has more-regularly arranged zooids in narrower branches and smaller, simpler avicularia.

The Chatham Island species is the youngest in the genus, extending its Upper Campanian-Lower Danian range by ca. 5 MY, and the first record outside Europe.

### Genus ***CHONDRIOVELUM*** Hayward & Thorpe, 1988

TYPE SPECIES. *Labioporella adeliensis* Livingstone, 1928, by original designation; Recent, Antarctica.

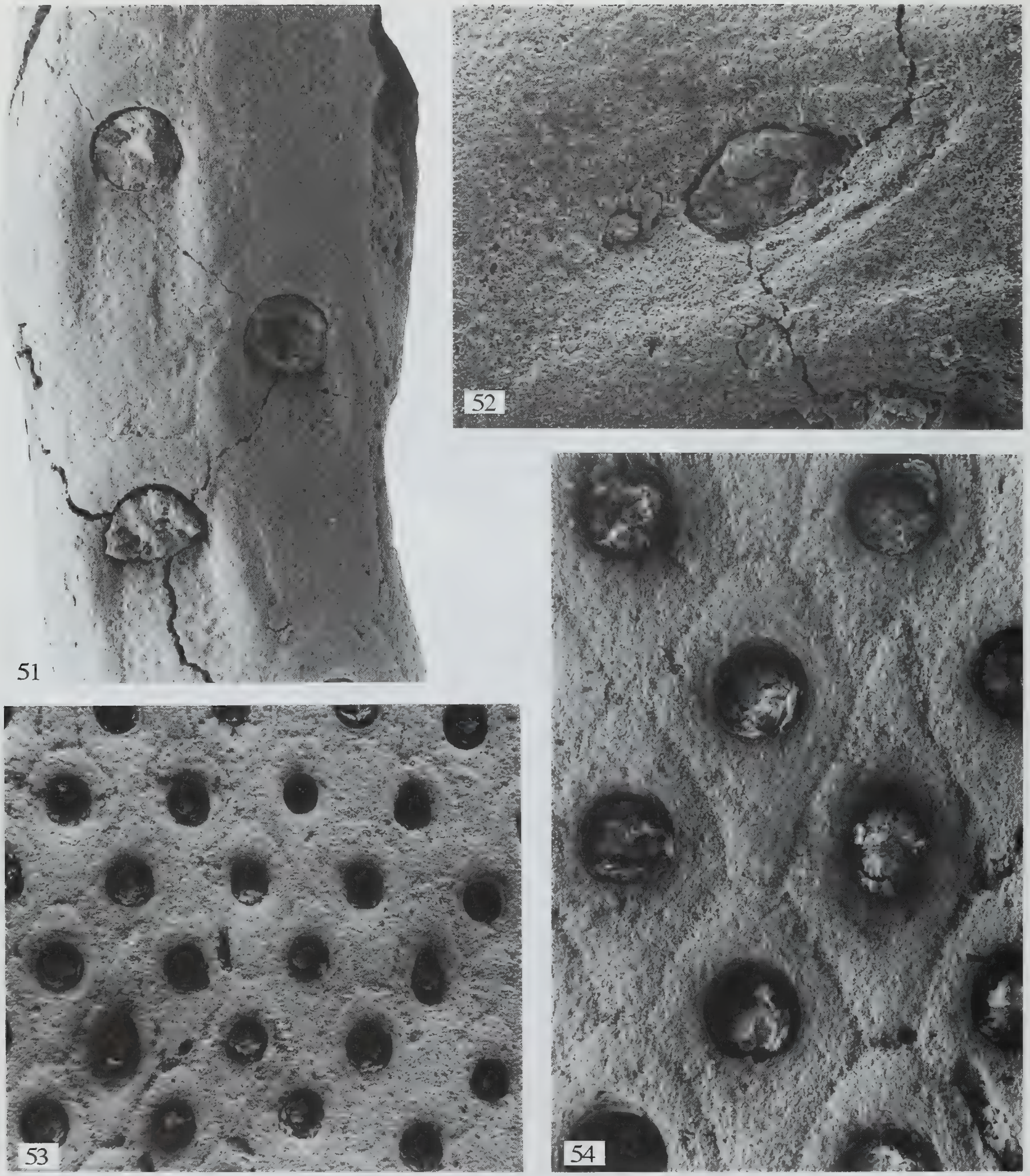
***Chondriovelum fossilis*** sp. nov. Figs 48–52

HOLOTYPE. IGNS BZ 188–1, from Pukekio, Chatham Island.

PARATYPES. IGNS BZ 188–2, 188–3, 188–4, 188–5.

DESCRIPTION. Colony erect, dichotomously branching, the stems more-or-less cylindrical except for a slight flattening at a bifurcation, 0.44–0.76 mm in diameter, being widest before a bifurcation. Zooids more-or-less alternating, in 6–8 longitudinal series, the larger number occurring before a bifurcation, reducing to 6 immediately after. Autozooids relatively elongate, length = 0.44–0.74 mm, width = 0.20–0.32 mm, the boundaries marked by narrow grooves between adjacent raised cryptocystal margins. Cryptocyst shallow, sloping to the opesia-orifice, the imperforate surface lightly reticulated in the best-preserved zooids. Opesia-orifice wider (0.11–0.19 mm) than long (0.07–0.13 mm), more-or-less bean-shaped with the middle part of the proximal rim slightly projecting as an inverse crescent, the ends of which appear as denticles. Large avicularia occasionally present, shorter than autozooids but occupying their place in a longitudinal series, with the autozooid distal to an avicularium longer and/or wider than other autozooids; the rostrum acute, with an area of palate encircling a longitudinally oval palatal foramen that is separated by a bridge of calcification from a tiny circular opesial foramen; proximal end of the avicularium truncate, the boundary slightly curved around the proximal autozooid. Ovicells not definitely seen; one zooidal orifice has a distal depression occluded with debris but its nature is equivocal.

REMARKS. The generic placement of this species is problematic. The shape and size of the opesia-orifice and the equivocal ovicellular depression are indicative of a cellariid affinity; on the other hand, some onychocellids can have relatively small opesiae. The large avicularium is very similar to that seen in Recent *Chondriovelum adeliense* (Livingstone) and *C. angustilobata* (Moyano) (family Onychocellidae) from Antarctica and magellanic South America,



**Figs 51–54** Onychocellid cheilostomes. **51–52,** *Chondriovelum fossilis* sp. nov.; **51,** IGNS BZ 188–4, branch fragment; notice reticulation of cryptocyst, × 211; **52,** IGNS BZ 188–5, vicarious avicularium, × 162. **53–54,** *Ogiva incompta* sp. nov., IGNS BZ 189–1, **holotype**, part of large colony fragment showing disposition of autozooids and vicarious avicularia, × 41 and × 87 respectively.

respectively (Moyano 1974; Hayward & Thorpe 1988). In this genus the avicularium also has both rostral and opesial foramina, although they tend not to be regular in shape.

There are some similarities with the monotypic Antarctic aspidostomatid genus *Larvapora* Moyano in the form of the orifice and the vicarious avicularium. *Larvapora mawsoni* (Livingstone) has folded bilamellar colonies, however, projections from the distal rim of the orifice, and elevated rostral rims. It also has distinctive ovicells. When definite ovicells are discovered in *C. fossilis* they should clarify the taxonomic position of this species.

### Genus *OGIVA* Jullien, 1882

TYPE SPECIES. *Eschara actaea* d'Orbigny, 1851; by original designation; Coniacian, Fécamp, France.

REMARKS. Originating in the Cenomanian (Taylor, 1993), the family Onychocellidae is especially well represented in the Late Cretaceous by a bewildering number of species whose colonial, autozooidal, and avicularian characters seem to intergrade to such an extent as to defy clear circumscription into genera. Such is also the case among the Cenozoic forms which are, however, relatively less diverse. In his voluminous work on the Cretaceous bryozoan faunas of France, d'Orbigny (1851–54) distributed the species, among which are encrusting, branching-cylindrical, and bilamellar forms, between several 'form-genera' based on colonial morphology. As Canu (1900) pointed out in his revision of this work, d'Orbigny often failed to account for ontogenetic variation in the appearance of zooids, and the illustrations accompanying the descriptions were often inexact, so that both he and Pergens (1889), who had attempted to revise the cyclostomes, frequently had difficulty in matching illustrations with specimens.

Jullien (1882) introduced the family Onychocellidae, the genera *Onychocella*, *Ogivalina*, *Floridina*, and *Smittipora* with Recent type species, and four other genera (*Ogiva*, *Dictuonia*, *Collura*, and *Rhebasia*) based on d'Orbigny species. The genera were distinguished, not primarily by colonial morphology, but by zooidal, opesial, and avicularian characters. A few years later, Koschinsky (1885) added *Rhagasostoma*, with an Eocene type species. Canu (1900) merged *Dictuonia, Collura,* and *Rhebasia* in *Ogiva* (which has page priority in Jullien 1882) on the grounds that the range of zooidal morphologies represented by these genera varies according to the ontogenetic age of the zooid and more than one such morphology can occur in the same colony – 'La forme colluréenne est toujours un signe de vieillesse; une ogivalia passe rapidement soit en dictuonia soit en rhebasia; c'est encore un signe de vieillesse. Les formes dictuonienne ou rhébasienne envahissent parfois tellement une espèce que la forme ogivalienne jeune est très rare' (Canu 1900: 387–388). Complicating an appreciation of the validity of the four Jullien genera based on species of d'Orbigny (1851) (and which influenced Canu's conclusions) is a lack of definitive knowledge of those species. *Eschara aceste* (type species of *Dictuonia*) was lacking from the collection when Canu revised it, and the specimen and illustrations of *E. actaea* (type species of *Ogiva*) did not correspond (Canu 1900: 420); *E. dorilas* (type species of *Rhebasia*) and *E. athulia* (type species of *Collura*) were represented by worn specimens only. A thorough revision of the d'Orbigny collection using scanning electron microscopy of all available material is critically needed. Pending such a revision, and its impact on the classification of onychocellids, the genus name *Ogiva* is used here for the following new species.

### ***Ogiva incompta*** sp. nov. Figs 53–56

HOLOTYPE. IGNS BZ 189–1, from Pukekio, Chatham Island.

PARATYPE. IGNS BZ 189–2.

NAME. From the Latin, *incomptus*, unadorned, referring the plain appearance of the zooids.

DESCRIPTION. Colony erect, comprising narrow to moderately wide bilamellar stems that broaden, in the two fragments available, from 1.08 mm diameter to 3.70 mm wide. Autozooids generally 'dictuonian', i.e., regularly 4-sided, alternating and arranged very evenly in oblique rows in the narrow-based fragment; most zooids very slightly rounded at distal and proximal ends, with some drawn out proximally and approaching the 'rhebasian' form in the broader, more worn fragment; length = 0.41–0.65 mm, width = 0.33–0.43 mm. Zooidal boundaries marked by a shallow but distinct furrow, the cryptocyst neither smooth nor granular in the present material, sloping inwards on all sides to the more-or-less centrally placed circular to subcircular opesiae (0.14–0.19 mm long, 0.14–0.17 mm wide). No spine bases or other features. Avicularia vicarious, perfectly replacing autozooids in a series without disrupting the regularity of oblique rows, almost identical to autozooids in appearance and width (0.31–0.37 mm) but distinguished from them by: (1) their slightly greater relative length within rows (0.54–0.77 mm) such that the acute rostral tip overlaps the proximal end of the distal autozooid, making that end W- instead of V-shaped; and (2) a more longitudinally oval opesiae (0.18–0.22 mm long, 0.11–0.14 mm wide). Lateral margins of colony comprising both autozooids and avicularia. No enlarged brooding or ovicelled zooids seen.

REMARKS. Although differing in size, the two fragments are sufficiently alike in zooidal characters to be considered as conspecific. The smaller, paratype fragment (Fig. 55) has an almost circular diameter proximally, broadening to bilamellar distally, with slightly smaller zooidal dimensions overall than the larger, holotype fragment (Fig. 53), which being broader and therefore certainly more distal in a colony would be expected to have incrementally larger zooid sizes. The larger fragment also lacks lateral margins so would have been broader in life than its current maximum breadth of 3.70 mm.

Brown (1958), without comment on the status of the genus, attributed two Tertiary Victorian species to *Ogiva*: *Membranipora concamerata* Waters, 1881 (Janjukian-Balcombian = Chattian-Langhian) and *Omoiosia elongata* Canu & Bassler, 1935 (Balcombian). The former species has slender, cylindrical branching stems and may represent a new genus of Onychocellidae; the latter species is definitely congeneric with *O. inornata*, from which it differs in having more longitudinally oval opesiae set in the distal half of the cryptocyst. (Based on the type species, *Omoiosia* Canu & Bassler, 1927, is, as Brown (1958) pointed out, a junior subjective synonym of *Chaperia* Jullien, 1881.)

### Genus *ONYCHOCELLA* Jullien, 1882

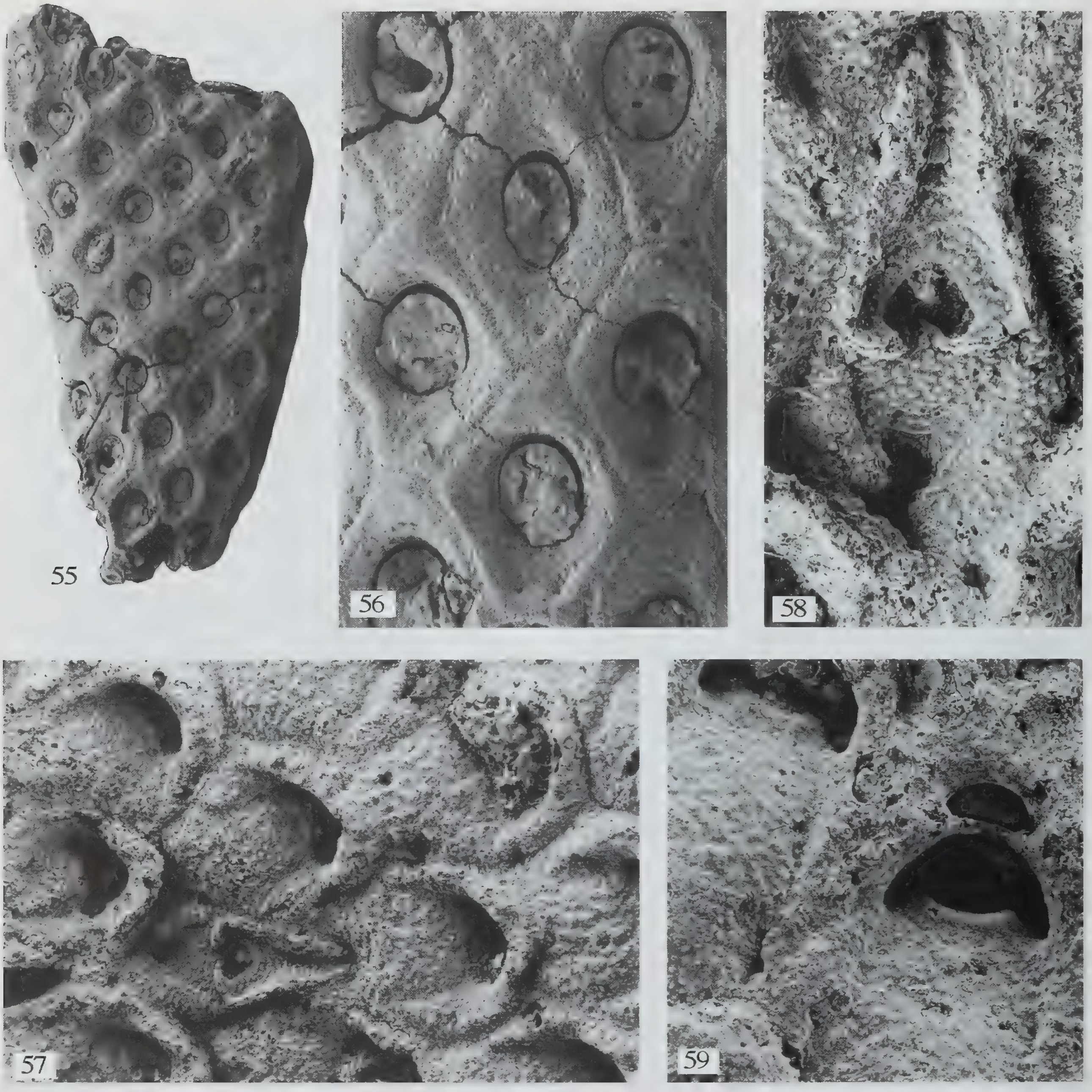
TYPE SPECIES. *Onychocella marioni* Jullien, 1882, by original designation; Recent, Cape Verde Islands to France and the Mediterranean, = *Cellepora angulosa* Reuss, 1848; Badenian (Langhian-Serravallian), Nußdorf, Austria (see Harmer 1926).

### ***Onychocella? lamellosa*** sp. nov. Figs 57–59

HOLOTYPE. IGNS BZ 190, from Pukekio, Chatham Island.

NAME. From the Latin *lamella*, a thin plate, veneer, alluding to the layered nature of the colony from self-overgrowth.

DESCRIPTION. Colony encrusting, self-overgrowing. Autozooids arranged quincuncially, sometimes almost as broad as long, length = 0.65–0.84 mm, width = 0.43–0.65 mm, with the lateral margins and especially the distal rim thickened and raised. Frontal cryptocyst granular, the opesia-orifice wider (0.21–0.26 mm) than long, the proximal rim broadly and narrowly anvil-like and slightly upturned, with rounded opesiular indentations at the corners. Avicularium



**Figs 55–59** Onychocellid cheilostomes. **55–56**, *Ogiva incompta* sp. nov., IGNS BZ 189–2, **paratype**, neanic colony showing disposition of autozooids and vicarious avicularia, × 51 and × 84 respectively. **57–59,** *Onychocella*? *lamellosa* sp. nov., IGNS BZ 190, **holotype**; **57,** autozooids and avicularium, × 58; **58,** close–up of avicularium, × 129; **59,** zooid with entrance to concealed ovicell, × 109.

subvicarious, occurring sporadically at the bifurcation of zooid rows but not every new zooid row starts with an avicularium; 0.65–0.71 mm long and 0.35–0.45 mm wide, the acute rostral tip overlaps the proximal end of the distal autozooid, making that end W-instead of V-shaped; rostral foramen subtriangular, bordered proximally by a stout pair of ridge-like pivots that do not fuse medially to form a cross-bar; no opesial foramen. Ovicells immersed under the cryptocyst of the succeeding zooid, visible as a slight bulge, with a narrow transverse opening just distal to the opesia-orifice of the maternal zooid. Lateral communication pore areas recessed between slight buttresses of inner autozooidal walls.

REMARKS. The zooidal and especially the opesial characters of this species are as much aspidostomatid as onychocellid, and the generic and family attributions are uncertain. Nevertheless, it is clear from the literature that there has been (and remains) considerable difficulty in distinguishing generic and, hence, familial boundaries in the large range of fossil species attributed to *Onychocella sensu* *lato*, related genera, and aspidostomatids. A perusal of a range of literature covering Late Cretaceous and Tertiary onychocellids and aspidostomatids (e.g., Brydone 1930; Voigt 1930, 1949, 1957, 1962, 1967, 1968, 1975, 1979, 1981, 1983, 1985b, 1987, 1989; Berthelsen, 1962) shows that a very wide range of colonial, zooidal, opesial, larval-brooding, and avicularian morphologies have been attributed to *Onychocella* alone. These include encrusting, erect uni- and bilamellar, and erect cylindrical and quadrilateral colony forms, broad subcircular to transversely narrow opesiae, nonexistent to vestigial to hyperstomial ovicells, and large and small, symmetrical to asymmetrical avicularia. Theoretically, heterochrony during zooidal ontogeny could account for all or most of this variation, but it is likely that, within the huge and bewildering array of species of *Onychocella sensu lato*, fine-grained statistical analysis would identify a number of clades, some of which would correspond to the variety of generic concepts within the family.

The type species of *Onychocella* is encrusting, the opesiae are relatively large and somewhat bell-shaped in outline, the 'ovicells' are endozooidal, and the avicularium is asymmetrical, with the rostral tip reflexed against the distolateral corner of an adjacent autozooid and the mandible unimembranous (i.e., on one side of the rachis only, the other half of the membrane being suppressed on the reflexed side of the rostrum). The nominal type species is *Onychocella marioni* Jullien, 1882, Recent, distributed from the Cape Verde Islands to France and the Mediterranean. Unquestionably this is a junior synonym of *O. angulosa* (Reuss, 1848), first described from the Austrian Tertiary (see Harmer 1926, and compare scanning electron micrographs of Recent (Hayward 1974) and fossil (Schmid 1989) material). Schmid's (1989) illustrations show more clearly than those of other authors that the avicularia have distinct, but weakly-developed mandibular pivots at the widest part of the avicularium. There is little information on the arrangement for larval brooding in *O. angulosa*. If it is the same as in *Floridina levinseni* Canu & Bassler (type species of *Velumella* Canu & Bassler, 1917), then there is no ovicell as such, just a cap-like overhang of the proximal end of the next zooid in the series (see Levinsen 1909: pl. 24, fig.10). In the sum of their characters, *Semieschara* d'Orbigny (type species *S. flabellata* d'Orbigny, 1852) and *Rhagasostoma* Koschinsky (type species *R. hexagonum* Koschinsky, 1885) accord with those of *Onychocella* as conservatively based on *O. angulosa* and these genera may be considered as synonyms.

How stable are the above morphological characters? The form of the avicularium and mandible appear visually distinctive, but Hastings (1930) has shown remarkable variation in the form of the mandible, at least, in *O. alula* Hastings, confirmed by Cook (1985). In this species most avicularia are skeletally symmetrical and the majority of the mandibles straight but, surprisingly, unimembranous. Occasionally the rachis may be set obliquely with a slight development of a membrane opposite the larger membrane. In older parts of colonies the thin and fragile membrane is normally lacking altogether. The evidence from this species, then, is that symmetrical avicularia need not imply bimembranous mandibles (as in *Smittipora* Jullien, 1882 and *Rectonychocella* Canu & Bassler, 1917 (a probable synonym of *Smittipora*)). Skeletally, the distal deflection of the avicularian rostrum is a variable character also. In several Cretaceous species attributed to *Onychocella* the avicularium may be symmetrical with no distal curvature, or have varying degrees of curvature, within the same colony (see for example, Voigt 1989). Mandibular pivots are lacking in many species attributed to *Onychocella* – it may be that the occurrence and shape of these is a useful character, along with the shape of the avicularian opesiae, but little study has been made. Frequently, published photographs and micrographs are not of adequate quality or magnification to give detailed information on some avicularian characters.

The presence of hyperstomial ovicells has been taken to be a 'good' character. Thus their occurrence in Recent '*Rectonychocella*' *disjuncta* Canu & Bassler, 1930 led Hayward (1974) to state that a new genus is required for this species. The presence of hyperstomial ovicells, and their consistent occurrence in erect cylindrical colonies in several species has allowed for the discrimination of *Latereschara* d'Orbigny, 1851 (Brydone 1930; Voigt 1959, 1967), which appears to be a 'good' genus. *Cheethamia* Shaw, 1967 also has hyperstomial ovicells but is encrusting. Scanning electron microscopy of the type species of both of these genera is needed to determine if they are congeneric. *Semiescharellina* d'Orbigny, 1852 (type species *S. mumia* d'Orbigny, 1852) may also be a synonym. Voigt (1989: 54) used *Cheethamia* subgenerically for a species of *Onychocella*.

The present species is excluded from *Cheethamia* in having transversely narrow opesiae with distinct opesiular indentations, well-developed articular ridges in the avicularium (lacking in *Cheethamia*), and a separate ovicell opening (not cucullate as in *Cheethamia*). Large subvicarious avicularia are not characteristic of *Aspidostoma* so the present species cannot be included in that genus – in the type species, *A. giganteum*, they are proportionately much smaller and interzooidal; they have similar articular ridges but a separated avicularian opesia (Hayward 1995).

### ?*Onychocella* sp. Figs 60–63

MATERIAL. IGNS BZ 210, a single eroded colony from Pukekio, Chatham Island.

DESCRIPTION. Colony encrusting. Autozooids arranged quincuncially, mostly longer than wide; length = 0.44–0.62 mm, width = 0.20–0.22 mm, with the lateral margins and periopesial rim thickened and raised. Frontal cryptocyst of an even level below the rim, the opesia-orifice high-arched in regular autozooids, generally as wide as long (0.13–0.19 mm), proximal rim with rounded opesiular indentations at the corners. Avicularium subvicarious, occurring sporadically at the bifurcation of zooid rows but not every new zooid row starts with an avicularium; 0.48–0.50 mm long, the broad lingulate rostrum either rounded distally or subacute, with an extensive palate; an indentation occurring on each side approximately half-way along the avicularium; a single, elongate-oval medial foramen. Ovicells hyperstomial, the narrow transverse opening separated from the zooidal opesiae by the distal rim of the zooid and apparently unable to be closed by the zooidal operculum in life.

REMARKS. As with the preceding species the generic and familial attributions of this species are uncertain. In both species the clear separation of the ovicellular opening from the opesia-orifice is not compatible with *Onychocella sensu stricto*.

## Genus INCERTAE SEDIS

### Onychocellid sp. not figured

MATERIAL. IGNS BZ 211, a single colony fragment from Pukekio, Chatham Island.

DESCRIPTION. Colony encrusting? Autozooids large, exceedingly thick-walled. Measured from orifice to orifice at the colony surface the zooids are 0.73–0.92 mm long, but internally one zooid is only 0.52 mm long between orifices whose length at the surface is 0.73 mm. This appears to be a consequence of the convex colony surface in the sole fragment whereby, as the zooidal cryptocysts thickened frontally in life, the peristomial orifices became more separated.

**Figs 60–64** Onychocellid and aspidostomatid cheilostomes. **60–63,** ?*Onychocella* sp., IGNS, BZ 210; **60,** eroded colony showing disposition of autozooids, ovicellate zooids and vicarious avicularia, × 45; **61,** vicarious avicularium and ovicellate zooid, × 95; **62,** vicarious avicularium, autozooidal and ovicelled orifices, × 127; **63,** ovicellate zooid (ovicell partly broken) and tip of avicularian rostrum proximally, × 116. **64,** *Aspidostoma litotes* sp. nov., IGNS BZ 191, **holotype**, part of erect branch, × 53.

Colony surface in the somewhat worn specimen rather featureless, with no trace of avicularia or other polymorphs. Peristomial and primary orifices more or less D-shaped or the proximal rim with a slight median convexity, 0.31–0.39 mm wide externally, 0.31–0.34 mm wide internally at the level of the primary orifice, with an indication in some orifices that slight opesiular indentations at the proximal corners continue as grooves down the inside of the peristome on each side. No indication of ovicells.

REMARKS. The generic affinities of this specimen are very obscure. The excessive thickness of the cryptocyst is reminiscent of *Inversaria*, but opesiae and orifices in *Inversaria* species are typically subcircular and more centrally placed. More and better-preserved material is needed.

## Family **ASPIDOSTOMATIDAE** Jullien, 1888

### Genus ***ASPIDOSTOMA*** Hincks, 1881

TYPE SPECIES. *Aspidostoma crassum* Hincks, 1881 = *Eschara gigantea* Busk, 1854, by monotypy; Recent, SouthAtlantic, Patagonia to Gough Island and the Antarctic Peninsula.

### ***Aspidostoma litotes*** sp. nov. Fig. 64

HOLOTYPE. IGNS BZ 191, from Pukekio, Chatham Island.

NAME. From the Greek, *litotes*, f., plainness, simplicity.

DESCRIPTION. Colony erect, cylindrical, evidently bifurcating, 0.54–0.80 mm diameter. Autozooids arranged in 5–8 longitudinal rows, the number of rows increasing distally, by row bifurcation, as a stem thickens. Autozooid length = 0.56–0.86 mm, width = 0.35–0.45 mm. Zooids widest in the vicinity of the orifice, each with thick, raised, rounded lateral rims that converge distally around the orifice. Frontal cryptocyst between the rims sloping towards the orifice, the surface granular where well-preserved. Opesia-orifice subrounded, the centre of the proximal rim gently concave with a tiny projection on each side defining a very small opesiular indentation. Avicularia and ovicells not seen.

REMARKS. Although lacking avicularia and ovicells, the zooidal and orificial characters of this species are similar to those of Runangan-Whaingaroan (Priabonian-Rupelian) *Aspidostoma curvatum* Uttley, 1949 and *A. turricula* Brown, 1952 from Oamaru which, however, have orifices opening on one face only. The lack of avicularia may be a genuine feature of *A. litotes*, or they may simply be rare as in *A. turricula*. There are some superficial similarities between *A. litotes* and a species from the Paleocene of Surinam described by Lagaaij (1969) as '*Vincularia' cristata*. However, the opesiae of Lagaaij's species have small pectinate denticles.

### ***Aspidostoma cinnabarina*** sp. nov. Figs 65–70

HOLOTYPE. IGNS BZ 192, from Pukekio, Chatham Island, encrusting a bivalve shell. No paratypes.

NAME. From the Latin *cinnabaris*, cinnabar, and Greek *kinnabarinos*, red like cinnabar, alluding to the red-coloured tuff at the type locality.

DESCRIPTION. Colony encrusting, large. Autozooids large, arranged quincuncially; length typically about 1 mm but ranging from 0.39 mm in zooids from zone of change to 1.14 mm in abnormal zooids; width usually 0.54–0.57 mm, but ranging from 0.45 mm in zooids from zone of change to 0.78 mm in zooids preceding row bifurcations. Frontal wall ventricose, sloping evenly all round, including distal to the orifice, into the deep interzooidal furrows, the surface regularly and evenly coarsely granular, the raised granules tending to be arranged into polygons so that the overall surface appears dimpled; there is a very slight elevation of the frontal wall immediately proximal to the orificial region. Opesia-orifice transversely narrow, the proximal rim straight with no or vestigial indentations at the corners, the distal rim and lateral peristome raised, with irregular tuberculation or processes; no oral spines. Small interzooidal avicularia occur generally sporadically, each at the junction of three autozooids, narrow with a narrow acute rostrum orientated proximally in the direction of the furrow; no apparent crossbar or condylar ridges. Ovicells hyperstomial, somewhat cucullate, the lateral margins raised, relatively straight and somewhat converging, the proximal rim tending to project over the opesia-orifice; external calcification interpreted as endooecium, relatively smooth. Basolateral septular communication pores set in narrow-buttressed recesses that simulate pore-chambers, budding intrazooidal in the terminology of Lidgard (1985). Reparative budding common, and autozooids with reversed orientation or completely closed and often kenozooidal.

REMARKS. *Aspidostoma cinnabarina* has virtually all of the characters typical of the Recent subantarctic type species of the genus, except for its overall robustness because of thick calcification, and appears easily accommodated in the genus. The interzooidal avicularia of the type species have a separate opesial foramen and are orientated obliquely distally, but these characters may be relatively trivial at the genus level in *Aspidostoma*.

## Family **CELLARIIDAE** Fleming, 1828

### Genus ***CELLARIA*** Ellis & Solander, 1786

TYPE SPECIES. *Farcimia sinuosa* Hassall, 1841, by synonymy (see Ryland 1968); Recent, NE Atlantic.

### ***Cellaria minus*** sp. nov. Figs 71–73

HOLOTYPE. IGNS BZ 193, from Pukekio, Chatham Island. No paratypes.

NAME: From the Greek, *minus*, little, small, short.

DESCRIPTION. Colony erect, evidently articulated in life, the internodes extremely slender, straight, 0.27–0.28 mm diameter. Autozooids alternating, in six longitudinal series, proportionately elongate and spindle-shaped longitudinally, tapering at both ends; length = 0.46–0.48 mm, width up to 0.22–0.24 mm across the widest part of the spindle. Zooidal boundaries defined by a common, thin, raised line of calcification. Cryptocystal surface evenly granular at low magnification, the granules looking like small tubercles at higher magnification. A shallow, longitudinally crescentic cryptocystal ridge occurs on each side frontally between the opesia-orifice and the lateral angle of the spindle, these converging but not uniting. The cryptocyst most sunken in the vicinity of the opesia-orifice is bean-shaped and wider (0.09 mm) than long (0.05–0.06 mm), with a short, truncate median convexity in the proximal rim. Orificial denticles or condyles not seen owing to occlusion of orifices by sediment in the unique specimen. Avicularia and ovicells not seen.

REMARKS. The unique holotype internode is well preserved but, owing to its fragility, broke in two when transferring from an SEM stub to the welled slide in which it now resides. The distal end, possibly eroded, nevertheless appears to represent a branch locus owing to the angles of zooids on opposing faces of the internode.

Although this species is represented by a single specimen that is both infertile and lacks polymorphs, it is named here because of its excellent preservation and its distinctively tiny size. Only four Tertiary *Cellaria* species have been reported from New Zealand before (Brown 1952). The present material corresponds to none of these, nor to any of the approximately 21 species described from the Australian Tertiary (see Maplestone 1904; Brown 1958 – note that some of the species listed by Maplestone are now recognisable as belonging to other cellariid genera), most of which are larger.

### ***Cellaria perexigua*** sp. nov. Figs 74, 75

HOLOTYPE. IGNS BZ 194–1, from Pukekio, Chatham Island.

PARATYPE. IGNS BZ 194–2.

NAME. From the Latin, *perexiguus*, very small.

DESCRIPTION. Colony erect, evidently articulated in life judging from the slight but abrupt tapering of the proximal end of the holotype specimen, the internodes very slender with subparallel sides, more-or-less straight, and with or without a barely discernible sigmoid flexure, 0.31–0.37 mm diameter. Autozooids alternating, in six longitudinal series, proportionately elongate but fish- not spindle-shaped, i.e., with the distal end convexly rounded and the proximal end concavely rounded; length = 0.39–0.47 mm, width up to 0.22–0.24 mm at the widest part of the zooid. Zooidal boundaries worn in the present material, with no discernible raised boundary lines. Cryptocyst as in *C. minus*, but the lateral ridges converging to become continuous distally. Opesia-orifice more-or-less D-shaped, as wide as that in *C. minus* but proportionately longer (0.07–0.08 mm), with a small rounded denticle on either side of the proximal rim (but not in the corners) and lacking a median convexity. Avicularia not seen. Ovicells present, the opening somewhat semicircular (possibly eroded) and slanting upwards at an angle so that the distal rim of ovicellate zooids is higher than in autozooids; internode a little wider in diameter where ovicellate zooids occur.

REMARKS. *Cellaria perexigua* is almost as diminutive as *C. minus* and is likewise distinguished from the other Cenozoic Australasian species on the grounds of very small size. It closely resembles *C. minus* but may be distinguished from it by the shape of the autozooid (not spindle-shaped), the distal convergence of the cryptocystal ridges, and the lack of a median convexity in the proximal rim of the opesia-orifice, instead having a pair of small, separated denticles.

### ***Cellaria elementaria*** sp. nov. Figs 76–78

HOLOTYPE. IGNS BZ 195–1, from Pukekio, Chatham Island.

PARATYPES. IGNS BZ 195–2; NHM BZ 4784–4785.

NAME. From the Latin, *elementarius*, pertaining to first principles, i.e., a very typical *Cellaria*.

DESCRIPTION. Colony erect, probably articulated in life, the internodes 0.74–1.14 mm in diameter, parallel-sided for part of their length, but tending to widen distally where ovicells occur. Autozooids alternating, in 13–15 longitudinal series, unevenly hexagonal in shape with the proximal and distal sides shorter than the lateral angles of the hexagon; length = 0.29–3.47 mm, width up to 0.20–0.34 mm at the widest part of the zooid. Cryptocyst granular, the cryptocyst ridges confined to the zooidal margins, with thin furrows between adjacent zooids. Opesia-orifice more-or-less D-shaped, relatively large in proportion to the sunken part of the cryptocyst which it resembles in size, a little wider (0.13–0.19 mm) than long (0.09–0.11 mm), the median proximal rim slightly produced as a thin crescent (concave in the middle) whose ends delimit slight opesiular indentations at the corners of the orifice. Avicularia not seen. Ovicellate zooids 0.37–0.45 mm long including the ovicell (broken in the present material), whose diameter is a little smaller than that of the opesiae from which it is separated only by the thin distal wall of the zooid.

REMARKS. This unremarkable species appears not to be conspecific with any of the other Australasian Cenozoic members of *Cellaria*.

### ***Cellaria* aff. *depressa*** Maplestone, 1900 Figs 79–81

aff. 1900 *Cellaria depressa* Maplestone, 1900: 167, pl. 18, fig. 15.

aff. 1904 *Cellaria depressa* Maplestone; Maplestone: 193.

MATERIAL. IGNS BZ 212–214, from Pukekio, Chatham Island; two internodes definitely conspecific, with a third, somewhat larger, internode probably also of this species.

DESCRIPTION. The two smaller internodes: colony erect and articulated in life, internodes 2.19–2.40 mm long, widest distally (0.65 mm diameter), tapering proximally (0.41–0.52 mm diameter). Autozooids in 9–10 longitudinal series, rounded distally, truncate proximally; length = 0.32–0.47 mm, width = 0.24–0.30 mm, widest at mid-length where the lateral margins are acutely angled. Zooidal boundaries in the slightly eroded specimens marked by a thin shallow groove. Cryptocyst sunken for much of its length in the smaller, less-eroded, specimen, less so in the other specimen, surface granular, the cryptocyst ridges converging to become continuous distally. Opesia-orifice at the deepest part of the cryptocyst, a little wider (0.09–0.11 mm) than long (0.06–0.08 mm), the proximal rim with a thin, median, crescent-shaped section where the two ends of the crescent are expressed as small denticles. Avicularia not apparent. Fertile zooids sparse, marked by a conspicuous cavity (the front evidently broken) immediately distal to the zooidal orifice.

Third internode somewhat more eroded, 2.81 mm long, with a diameter of 0.70–0.84 mm, and 13 longitudinal series of autozooids. Zooidal dimensions as in the two smaller internodes, the orifices have an identical proximal rim but are slightly higher-arched, and the broken ovicells have the same appearance. One zooid near the proximal end of the internode may have been aviculiferous; it has an inverse pear-shaped opesia sunken in the centre, surrounded by concentrically arranged calcification.

REMARKS. If the larger, third internode obtained from the Red Bluff Tuff is conspecific with the two smaller internodes then the Chatham Island specimens have many of the characters of *Cellaria depressa* Maplestone, 1900 from Shelford and Campbell's Point, Victoria (Miocene) (Maplestone, 1904). Using the magnification scale in Maplestone (1900), a *C. depressa* internode measures 1.02 mm diameter and the zooids are 0.50–0.59 mm long, i.e., larger than the Red Bluff Tuff specimens, but the width of zooids and orifices is the same. It is likely that the Chatham Island material is not conspecific with *C. depressa*, but more specimens (with more characters) are needed of both the Chatham Island and Australian populations for a definite conclusion to be reached.

## Genus ***SMITTICELLARIA*** gen. nov.

TYPE SPECIES. *Cellaria tectiformis* Hayward & Cook, 1979.

DIAGNOSIS. Colony erect, branching in one plane, unjointed or with secondarily developed fractures at bifurcations that are secured by frontally produced rhizoids. Autozooids *Cellaria*-like, with transversely bean-shaped opesia-orifices and proximal pivots. Avicularia vicarious, with one occurring on the upper side of each bifurcation and others scattered elsewhere. Ovicell with the opening small, occurring within the distal border of the maternal zooid.

NAME. The name is a composite of *Smittipora* and *Cellaria*, alluding to the combination of morphological characters of these genera.

REMARKS. As Hayward (1995) has remarked, the classification of

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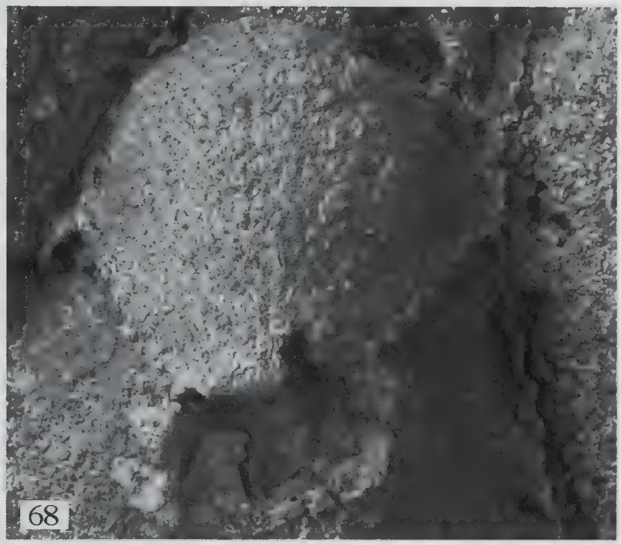
**Figs 65–70** *Aspidostoma cinnabarina* sp. nov., IGNS BZ 192, **holotype**. **65,** disposition of autozooids and ovicellate zooids, × 35. **66,** autozooidal orifice, × 290. **67**, ovicellate zooids, × 65. **68,** ovicell, × 170. **69,** boundary between opposing zooids (some missing), some of which are incompletely formed, × 32. **70,** interzooidal avicularium, × 250.


65


66


67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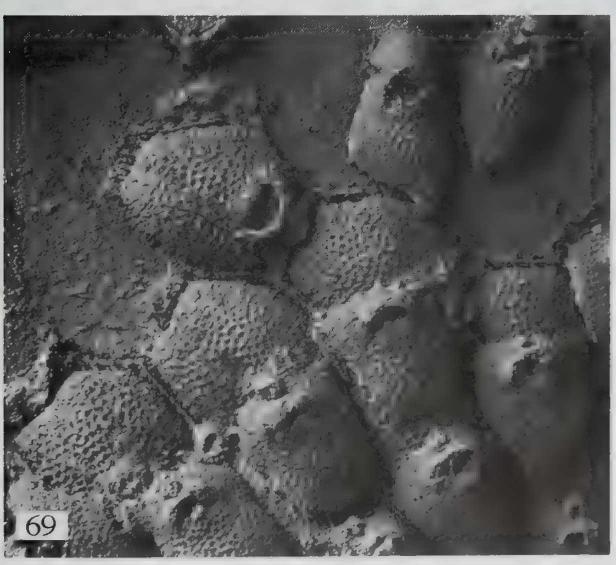
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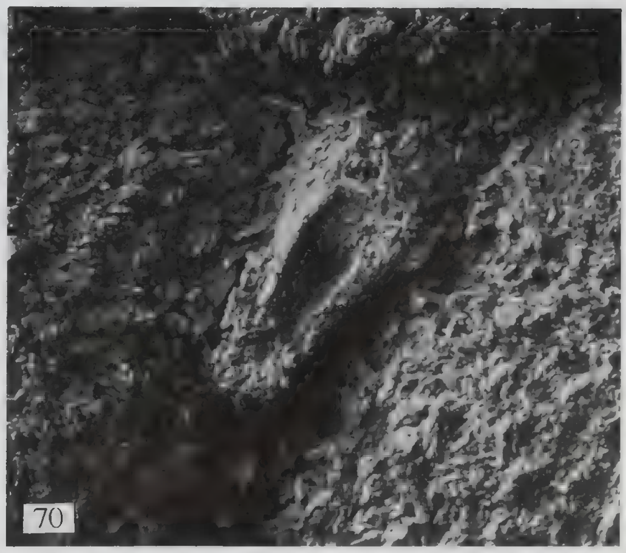
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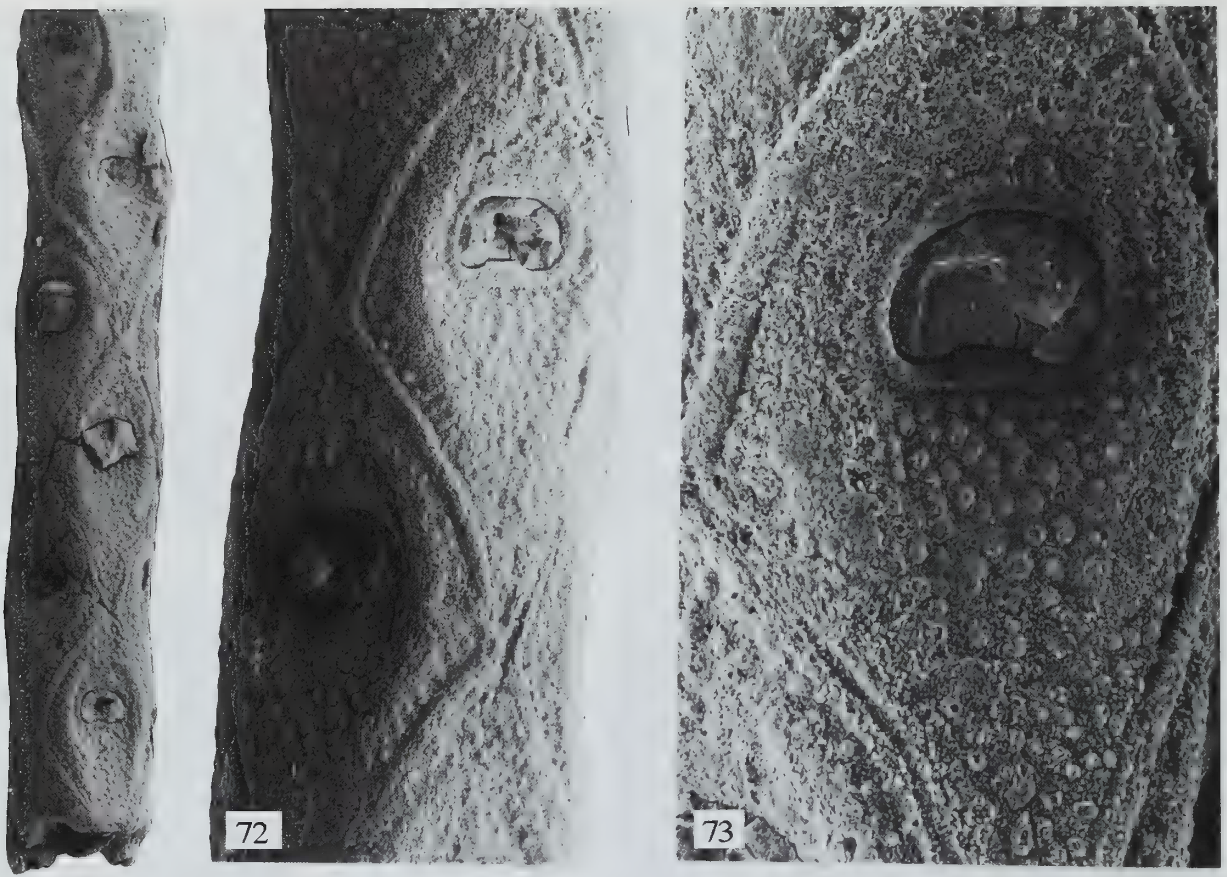


**Figs 71–73** *Cellaria minus* sp. nov., IGNS BZ 193, **holotype**; **71**, branch, × 62; **72**, alternating zooids, × 161; **73**, granular cryptocyst and opesia-orifice, × 304.

the Cellariidae is unsatisfactory, both within the type genus *Cellaria* Ellis & Solander and among a number of other genera insofar as their limits are not well circumscribed. Beginning with Busk (1884), attempts have been made to segregate species of *Cellaria sensu lato* into informal, or even formal, groupings based on various combinations of autozooidal shape, method of branching, and size of avicularium. Hayward (1995) pointed out the limitations of some of these attempts, but *Cellaria* as presently circumscribed is too broad in relation to the characters of the northeastern Atlantic type species.

The following new species, although based on limited material, is regarded as sufficiently similar in branching and avicularian characters to Recent *Cellaria tectiformis* Hayward & Cook, 1979 as to justify the establishment of a new genus based on these two species. The characters are: (1) all branching in a single plane; (2) bifurcations lacking articulations or, if an articulation develops, it is based on a subsequent fracture (and securing of both sides of the fracture by frontally produced rhizoids); (3) axial vicarious avicularia; and (4) complete lack of any mandibular pivots, ridges, or condyles. It is possible that additional fossil species may be attributable to *Smitticellaria*: Maastrichtian-Danian *Vincularia microstoma* Marsson, 1887 (Denmark and Germany) and Danian *Onychocella columella* Berthelsen, 1962 (Denmark and Germany) ought to be examined in this regard (see descriptions and illustrations in Berthelsen (1962) and Voigt (1987)).

Range. Thanetian to Recent.

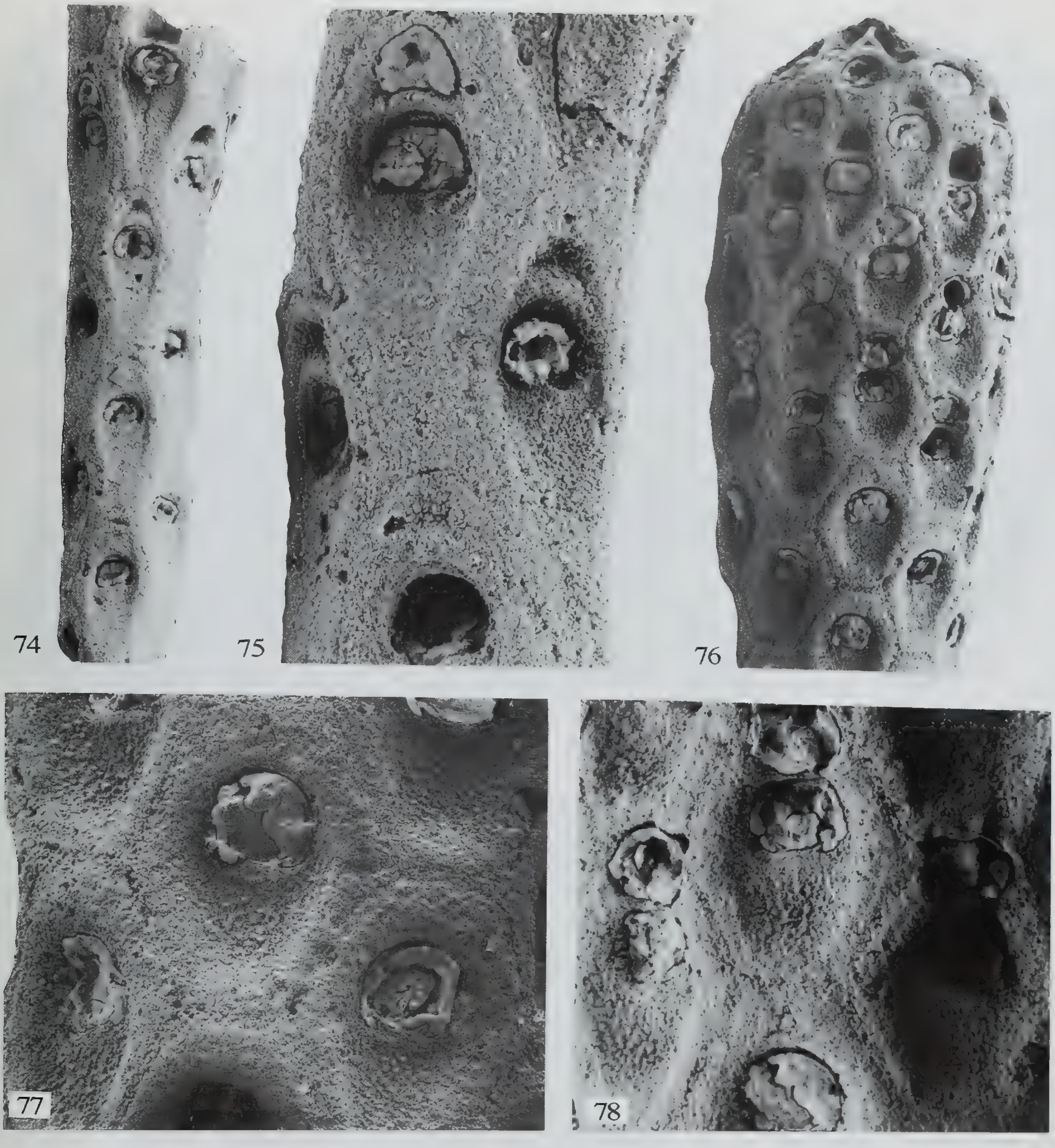
### ***Smitticellaria morioriana*** sp. nov. Figs 82–84

Holotype. IGNS BZ 196–1, from Pukekio, Chatham Island.

Paratypes. IGNS BZ 196–2, 196–3, 196–4.

Name. The name evokes the indigenous Polynesian inhabitants of the Chatham Islands, the Moriori.

Description. Colony erect, dichotomously branching, non-articulated, the stem and branches cylindrical, 0.33–0.49 mm in diameter. Autozooids alternating, disposed in 8 longitudinal series, reducing to 6 after a bifurcation, the boundaries evidenced by thin lines of calcification where well-preserved; shaped more-or-less like a 4-sided diamond with each corner acute or the distal and proximal ends very slightly rounded-truncate; length = 0.35–0.40 mm, width = 0.20–0.34 mm. Cryptocyst concave, more so towards the opesia-orifice, the surface minutely granular-tubercular where well-preserved. Opesia-orifice wider (0.09–0.10 mm) than long (0.06–0.07 mm), transversely bean-shaped, the proximal rim with an inversely crescentic part, the ends of which project as denticles. Vicarious avicularia occurring at a bifurcation in both the inner and outer angles; widest proximally, narrowing to a lingulate rostrum with an extensive palate and rounded tip; only a single subcircular foramen occurs in the centre of the avicularium. Ovicells with a small rounded opening occurring between the distal border and the opesia of the maternal zooid.



**Figs 74–78** Species of *Cellaria*. **74–75,** *Cellaria perexigua* sp. nov., IGNS BZ 194–1, **holotype**, × 52 and × 135 respectively. **76–78,** *Cellaria elementaria* sp. nov., IGNS BZ 195–1, **holotype**; **76,** distal end of internode showing widening diameter in the region of ovicelled zooids, × 49; **77**, autozooids, × 130; **78**, ovicellate zooids, × 109.

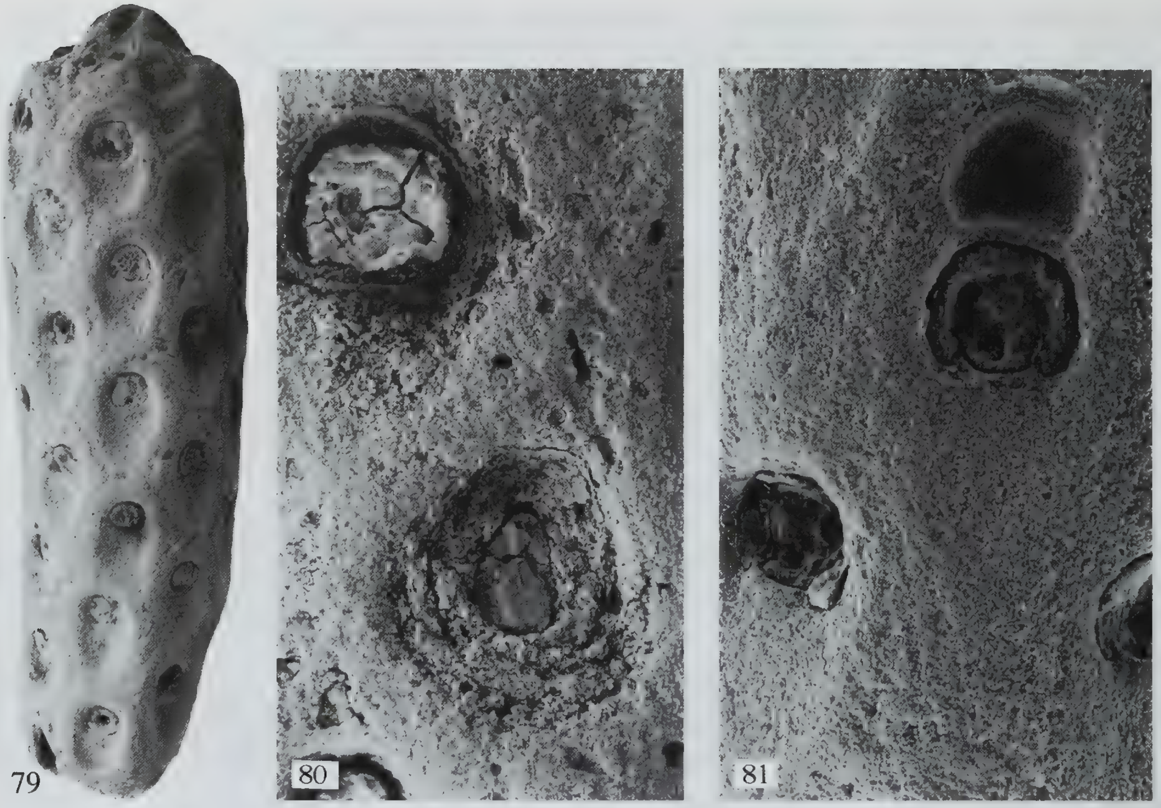
REMARKS. *Smitticellaria morioriana* differs most notably from the nominated type species, *S. tectiformis*, in having 6–8 longitudinal zooidal series (instead of four), a concave proximal opesial rim, and a more lingulate avicularian rostrum.

### Genus *ESCHARICELLARIA* Voigt, 1924

TYPE SPECIES. *Escharicellaria polymorpha* Voigt, 1924, by monotypy; Senonian, Germany.

?***Escharicellaria*** sp. Figs 85–87

MATERIAL. IGNS BZ 215, several specimens from Pukekio, Chatham Island.



**Figs 79–81** *Cellaria* cf. *depressa* Maplestone, 1900, IGNS BZ 212. **79,** internode, × 50. **80,** occluded autozooidal orifice and adjacent ?avicularium (lower right), × 210. **81,** orifice and cavity of an ovicell, × 160.

DESCRIPTION. Colony erect, comprising proximally tapered, narrow bilamellar stems that periodically produce narrower side branches. The larger colony fragment is 1.60–3.00 mm wide, lensoidal in cross section, with side branches ca. 1.49–1.61 mm wide. Zooids regularly alternating such that opesia-orifices occur in straight oblique rows, interzooidal boundaries not clearly discernible; length = 0.52–0.75 mm, width = ca. 0.32 mm; cryptocyst depressed, sloping inwards to the external opesia-orifice which is more-or less D-shaped, 0.14–0.19 mm wide; primary orifice sunken, the proximal rim shallowly concave with narrow but distinct opesiular indentations at the corners. Avicularia not seen. Ovicells in the present worn material broken, indicated by relatively deep cavities, each immediately distal to the opesia-orifice and separated from it by the distal rim of the maternal zooid; these cavities almost twice the height (length) of the subjacent opesia-orifice.

REMARKS. The specimens of this bryozoan are not well-enough preserved to name as a new species, especially as some morphological characters are lacking, but the colony form is distinctive enough to allow recognition should additional material be found. It shares some of the attributes of erect bilamellar forms of *Aspidostoma* but the unequal mode of branching (not regular bifurcations) and form of the orifice are more suggestive of cellariid affinity.

## Genus *MELYCHOCELLA* gen. nov.

TYPE SPECIES. *Melychocella cynura* sp. nov.

DIAGNOSIS. Colony erect, bilamellar, with somewhat hexagonal zooids arranged in continuous longitudinal series. Cryptocyst sunken, no ridges, the opesia-orifice wider than long with both proximal and distal condyles and small opesiular indentations. Scattered vicarious avicularia have rostral and opesial foramina. Ovicells large, the frontal surface not crossed by the outer angles of adjacent zooids.

NAME. The name is a composite of *Melicerita* and *Onychocella*, alluding to the combination of morphological characters of these genera.

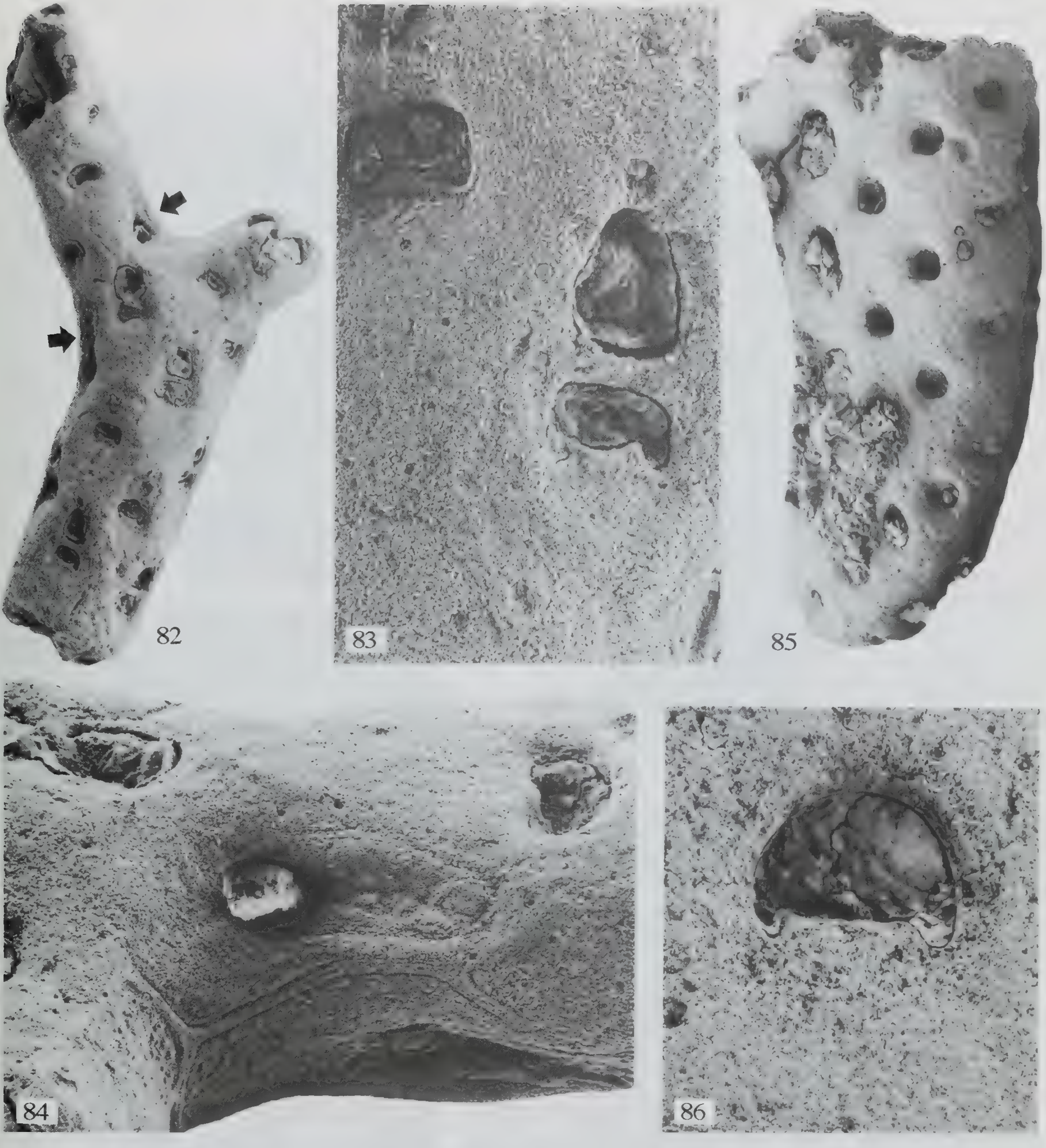
### *Melychocella cynura* sp. nov. Figs 88–92

HOLOTYPE. IGNS BZ 197–1, from Pukekio, Chatham Island.

PARATYPES. IGNS BZ 197–2, 197–3, 197–4. NHM BZ 4786.

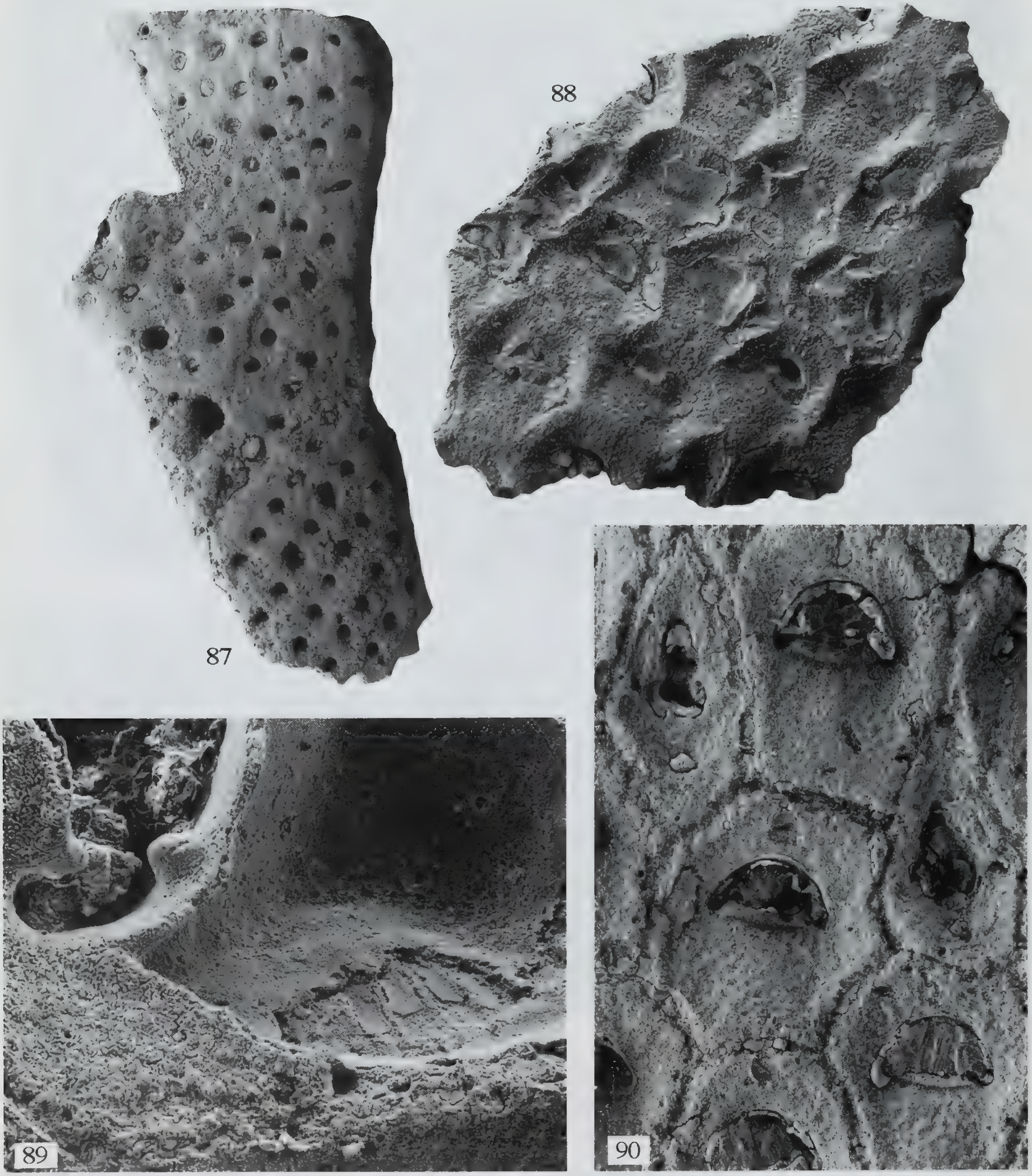
NAME. *Cynura* is a latinisation of the Greek *kynouron*, a sea-cliff, alluding to the type locality.

DESCRIPTION. Colony erect, bilamellar, 0.72–0.75 mm thick. Autozooids alternating, nearly hexagonal, averaging a little longer than wide (length = 0.44–0.56 mm, width = 0.37–0.52 mm) and clearly defined by the raised lateral margins, the longitudinal series continuous, not discontinuous. Cryptocyst completely sunken with no ridges, the surface distinctly granular. Opesia-orifice relatively large, wider (0.20–0.24 mm) than long (0.10–0.12 mm, as measured from middle to middle of each rim), with the corners extended a little proximally as rounded opesiular indentations, each being adjacent



**Figs 82–86** Cellariid cheilostomes. **82–84,** *Smitticellaria morioriana* sp. nov., IGNS BZ 196–1, **holotype**: **82,** part of colony, position of vicarious avicularia arrowed, × 48; **83,** ovicellate orifices, × 209; **84,** axillary vicarious avicularium, × 169. **85–86,** ?*Escharicellaria* sp., IGNS BZ 215; **85,** presumed small colony, × 22; **86,** autozooidal orifice, × 173.

to a rounded condylar process; a pair of distal condyles opposite the proximal ones. Generally a transverse groove parallel to the proximal rim of the opesia-orifice. Vicarious avicularia mostly occurring at the bifurcation of a zooid row, sometimes merely replacing an autozooid in a longitudinal series, 0.46–0.52 mm long and 0.21–0.26 mm wide; in the best-preserved examples they are granular-surfaced, widest at mid-length, with the rostrum parallel-sided before abruptly tapering acutely, the proximal end rounded; with a subtrifoliate palatal foramen and a very small circular or oval opesial foramen. Ovicells large, slightly recumbent on the distal zooid, the ovicellular chamber deep though not reaching the level of the basal walls of the maternal and distal zooids; frontal surface



**Figs 87–90** Cellariid cheilostomes. **87,** ?*Escharicellaria* sp., IGNS BZ 215, moderate-sized colony fragment with the proximal end of a broken branch at left, × 13. **88–90,** *Melychocella cynura* sp. nov.; **88,** IGNS BZ 197–2, autozooids and avicularia; note granularity of cryptocyst, × 43; **89,** IGNS BZ 197–3, part of ovicelled orifice showing proximal and distal denticles, and fabric of ovicell walls, × 270; **90,** autozooids and avicularia, IGNS BZ 197–1, **holotype**, × 88.

unknown owing to loss through breakage, but apparently not crossed by the angles of adjacent zooids, the opening separate from the opesia-orifice.

REMARKS. This striking species represents a new genus of Cellariidae. It appears closest to *Melicerita* Edwards *sensu stricto* from which it differs, however, in the occurrence of elongate vicarious avicularia with separate rostral and opesial foramina, and much larger combined female zooid and ovicell. As presently constituted, the genus *Melicerita* appears to need splitting. The Pliocene type species, *M. charlesworthii* Morris, 1843, has vicarious avicularia, with a large longitudinally oval foramen and no pivots, scattered throughout the colony; the ovicell is relatively small with no elaboration of calcification either side of the opening, and the opesia-orifices are not dimorphic (see Bishop 1987). Recent Tierra del Fuegian *M. temaukeli* Moyano, 1997 shares a number of characters with the type species. Antarctic *Melicerita latilaminata* Rogick, 1956 and *M. flabellifera* Hayward & Winston, 1994 have similar features, except that the avicularian foramen in both species has a proximal sinus either side of which is a shoulder for pivoting of the mandible. These latter two species could possibly be regarded as constituting a subgeneric clade within *Melicerita*. Several Australasian species (*M. angustiloba* Tenison-Woods, 1862, *M. chathamensis* Uttley & Bullivant, 1972, *M. knoxi* Uttley & Bullivant, 1972, *M. ejuncida* Gordon, 1986) have smaller, interzooidal avicularia confined to the lateral margins of the colony and the fertile zooids have dimorphic orifices with a complex pattern of surface calcification adjacent to the opening, sometimes with perforations. These species may constitute another subgeneric clade, to which should be added Antarctic *M. obliqua* (Thornely, 1924) and *M. blancoae* López Gappa, 1981 (which lack avicularia), and *M. digeronimoi* Rosso, 1992, all three of which lack dimorphic orifices but have the complex surface calcification. *Melicerita atlantica* Busk, 1884 and *M. antarctica* d'Hondt, 1984 (which may be conspecific – see Rosso 1992) differ in too many features to be included in *Melicerita sensu stricto*.

### Suborder **ASCOPHORINA** Levinsen, 1909
### Family **ARACHNOPUSIIDAE** Jullien, 1888

### Genus ***ARACHNOPUSIA*** Jullien, 1888

TYPE SPECIES. *Lepralia monoceros* Busk, 1854, by original designation; Recent, Patagonia.

***Arachnopusia gracilis*** sp. nov. Fig. 93

HOLOTYPE. IGNS BZ 198, from Pukekio, Chatham Island. No paratypes.

NAME. From the Latin *gracilis*, slender, alluding to the narrow bilamellar stem.

DESCRIPTION. Colony erect, gracile, with thin bilamellar stem 0.93–1.22 mm wide. Autozooids arranged more or less quincuncially, each being surrounded by 5–7 others; length = 0.37–0.60 mm, width = 0.14–0.24 mm; interzooidal boundaries merging and not clearly defined. Frontal shield more-or-less evenly perforated by 15–20 small, simple, circular to subcircular or oval foramina. Orifice 0.09 mm wide, somewhat bean-shaped owing to a median convexity of the proximal rim; peristome low (or eroded), the entire colony surface being relatively flat. No trace of distal or intraoral spines or spine bases. In interzooidal areas and/or distal to some orifices are small polymorphs; these appear to be kenozooids, but some may correspond to avicularia; of variable shape from oval to distally acute, with an inwardly sloping shelf of uniform width surrounding the central opesia, also of varying shape. Ovicells not apparent.

REMARKS. Only two other species attributed to *Arachnopusia* are known from the New Zealand Tertiary: *A. unicornis* (Hutton, 1873), ranging from Otaian (Lower Burdigalian) to Recent, and *A. bugei* Brown, 1952, occurring only in the Waiauan (Serravallian), Southland Series (Gordon *et al*., 1994). *Arachnopusia unicornis* is known to produce erect bilamellar colonies from an encrusting base but they are broad and foliaceous, the zooids have fewer, larger foramina, and the aviculiferous proximal rim of the peristome is less convex (Gordon 1989b). From SEM examination of the holotype specimen, *Arachnopusia bugei* appears not to belong to this genus at all – it lacks foramina in the centre of the shield. The combined characters of the shield and proximal 1–2 intraoral avicularia (not spine bases as interpreted by Brown) suggest inclusion in the Desmacystidae or Rhamphostomellidae (see Gordon & Grischenko 1994).

### Family **KLEIDIONELLIDAE** Vigneaux, 1949

### Genus ***PAVOBEISSELINA*** Voigt, 1964

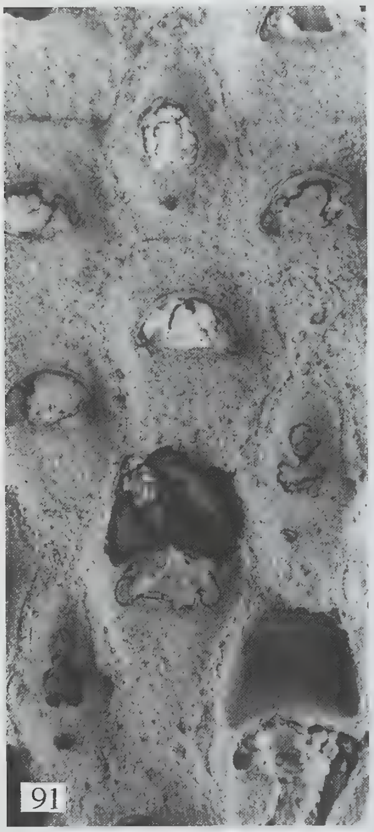
TYPE SPECIES. *Eschara oblita* Kade, 1852, by original designation; Paleocene, Germany.

**?*Pavobeisselina*** sp. Figs 94, 95

MATERIAL. IGNS BZ 216, a unique specimen from Pukekio, Chatham Island.

DESCRIPTION. Colony small, fan-shaped, bilamellar, evidently attached by rootlets in life; height of incomplete colony 3.6 mm; maximum width 4.1 mm; thickness 0.48–0.56 mm, being thicker towards base. Zooids appear to be arranged quincuncially based on the distribution of peristomial orifices but there are no zooidal boundaries at the colony surface; length = 0.41–0.47 mm (measured in longitudinal section on fractured part of colony), width not readily determinable. Peristomial orifices circular or subcircular, 0.14–0.17 mm in diameter, flush with colony surface. Other perforations comprise areolar pores (variable diameter); possible avicularia, lacking a crossbar but with a narrow concentric shelf below the surface; and the openings of possible spiraminal tubes, but, as is typical of this and related genera, the identity of the perforations is difficult to determine from their surface distribution alone.

REMARKS. The family and genus attributions are uncertain. One of us (DPG) has examined by SEM external and internal colony surfaces in the type species of *Kleidionella* Canu & Bassler, *Beisselina* Canu, and related genera of equivalent age. *Kleidionella* and *Beisselina* form erect colonies, often quite robust, from an encrusting base. Both genera have planar-spherulitic microstructure on the inner surface of the frontal shield; *Beisselina* has a characteristic suboral spiraminal pore and tube, lacking in *Kleidionella*. *Beisselina*, *Pavobeisselina*, *Pseudobeisselina* Wiesemann, *Beisselinopsis* Voigt, and a number of other Late Cretaceous-Paleogene genera have traditionally been attributed to the family Porinidae, but, based on an examination of the frontal shield of the Recent type species *P. gracilis* (Lamarck), *Porina* is characterised by a lepralioid ('cryptocystidean') frontal shield. Thus the so-called ascopore in *Beisselina* (see Wiesemann, 1963) is technically a spiramen since it does not open into a compensation sac. As indicated by Pouyet (1973), *Kleidionella* has some of the characters of several celleporiform genera (umbonuloid shield, large avicularia with cross-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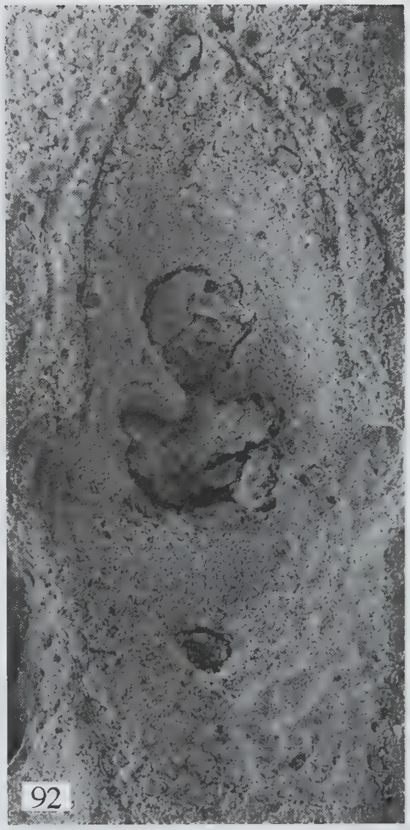
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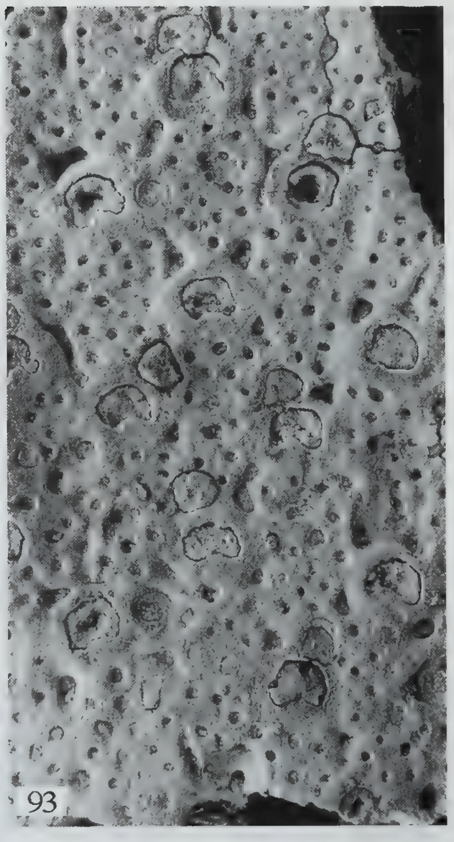
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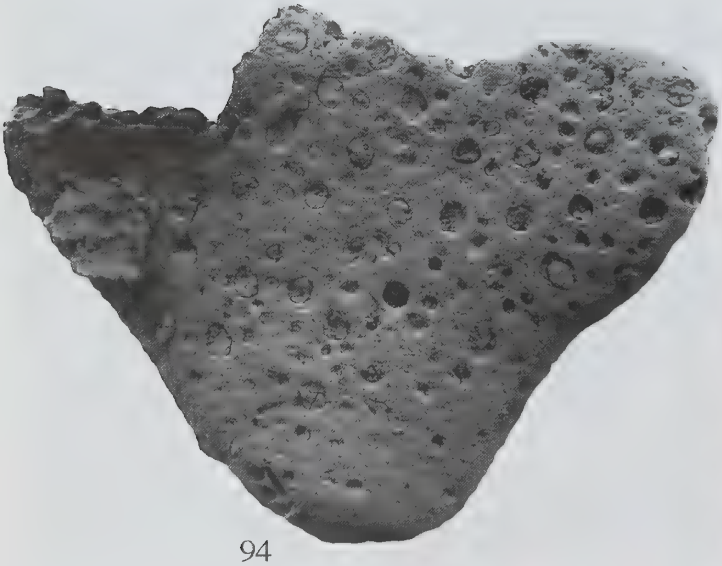
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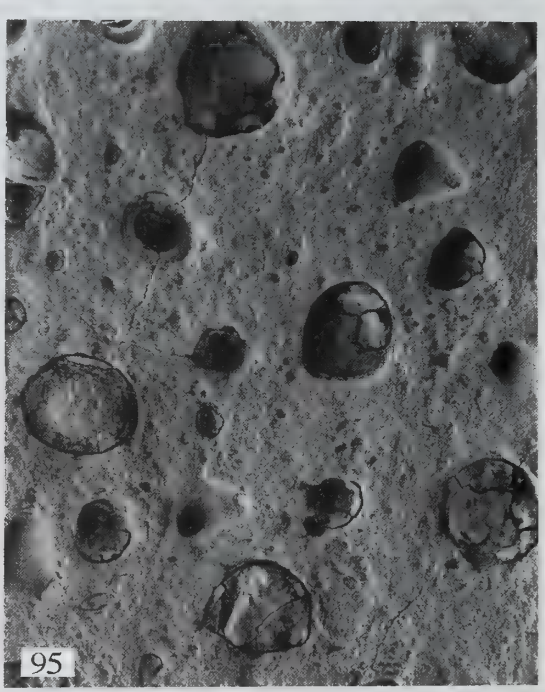
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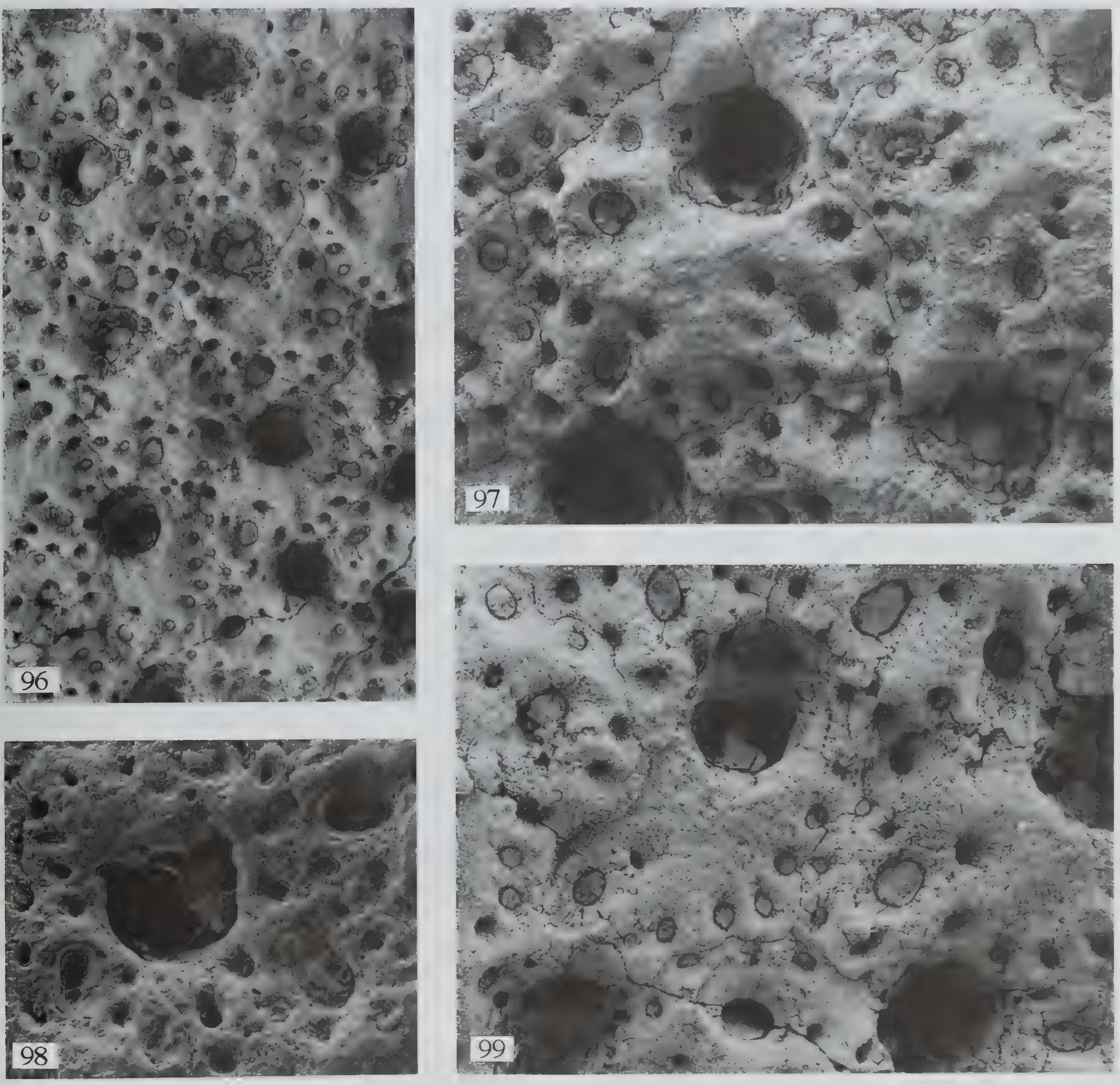
**Figs 91–95** Cheilostomes. **91–92,** *Melychocella cynura* sp. nov., IGNS BZ 197–4; **91,** autozooids, avicularia, and ovicellate zooids, × 56; **92,** vicarious avicularium, × 193. **93,** *Arachnopusia gracilis* sp. nov., IGNS BZ 198, **holotype**: autozooids, × 70. **94–95,** ?*Pavobeisselina* sp., IGNS BZ 216; **94,** bilamellar colony, tapering proximally, × 19; **95,** zooidal orifices and other perforations on the colony surface, × 79.

bars), but the surface expression of the peristomial orifices, areolar pores, and range of avicularian sizes of *K. grandis* Canu & Bassler has much in common with that of *Beisselina*. Kleidionellidae Vigneaux is therefore used here rather than create a separate family for *Beisselina* and similar forms.

*Beisselina* has not previously been associated with *Kleidionella* and the two genera would not historically have been associated because of the lack of a spiramen in the latter. The presence/absence of a spiramen need not require segregation at the family level, however, as evidenced by the following genus pairs: *Beisselina* / *Pseudobeisselina*, and *Beisselinopsis* / *Pavobeisselina*. *Pseudobeisselina compressa* (Goldfuss), type and only species of the genus, was formerly classified in *Beisselina* until it was discovered that it lacks an 'ascopore' – 'Sinus oder Spiramen, keine Ascopore' (Wiesemann, 1963: 51). *Beisselinopsis* and *Pavobeisselina* both have rooted fan-shaped colonies (by which they differ from *Beisselina*) but the former lacks a spiramen and the latter has one. In umbonuloid-shielded cheilostomes, however, it is a relatively simple matter to convert a peristomial pseudosinus into a spiraminal tube (this is how a spiraminal tube is formed ontogenetically) and there appears to be no intrinsic reason why, if other morphological characters conform, apparently related genera should be segregated on the basis of the spiramen alone. Traditionally, a pore associated with a peristome has been termed a spiramen, whereas a pore more



**Figs 96–99** *Hippopleurifera australis* sp. nov., IGNS BZ 199, **holotype**. **96,** disposition of zooids, × 58. **97,** autozooids; note the appearance of paired spine bases at the sides of the orifices, × 106. **98,** avicularia adjacent to the orifice (distal is towards the bottom of the photo), × 119. **99,** autozooids; note the areolar pores in the steeply descending cormidial orifices, × 116.

proximally placed in the frontal shield has been called an ascopore (hence Wiesemann's distinction), but in umbonuloid-shields this positional distinction has not the same relevance.

The presence of spiraminal openings in the Red Bluff Tuff specimen is equivocal on the basis of the surficial distribution of perforations. Although it was possible to view the proximal part of the frontal-shield interior of some zooids at the fractured colony edge, a more distally occurring inner spiraminal opening would have been missed. Thus the specimen may lack spiramina, in which case it could be included in *Beisselinopsis*. Voigt (1964: 452) describes young zooids in the type species, *B. hiltermanni* Voigt, as 'perforated by a considerable number of pores (?tremopores)' (see also Voigt 1962). More and better-preserved specimens from the Red Bluff Tuff are needed to settle the matter of generic assignment. Both of these genera are otherwise known only in the European Dano-Montian.

The French Paleocene species *Beisselina bigeyae* Braga & Bignot, 1986, shows some similarities with ?*Pavobeisselina* sp. but has smaller orifices.

## Family **ROMANCHEINIDAE** Jullien, 1888

### Genus ***HIPPOPLEURIFERA*** Canu & Bassler, 1925

TYPE SPECIES. *Eschara biauriculata* Reuss, 1848, by monotypy; Badenian (= Langhian (Serravallian), Eisenstadt, Austria (see Hastings 1966: 73).

REMARKS. *Hippopleurifera* is generally included in the family Umbonulidae (e.g., Hastings 1949; Bassler 1953; Cheetham 1968; David & Pouyet 1974; Schmid 1989); however, the occurrence of laterally emplaced avicularia (when present), general appearance of the frontal shield, and ovicellular calcification skeletally continuous with that of the frontal shield are much more characteristic of the closely related family Romancheinidae (cf. the genera *Escharoides* Edwards and *Exochella* Jullien).

### ***Hippopleurifera australis*** sp. nov. Figs 96–99

HOLOTYPE. IGNS BZ 199, from Pukekio, Chatham Island. No paratypes.

NAME. From the Latin *australis*, southern, alluding to the first occurrence of this genus in the Southern Hemisphere.

DESCRIPTION. Colony encrusting. Autozooids arranged more-or-less quincuncially and as wide as long or longer; length = 0.26–0.47 mm, width = 0.46–0.56 mm; the interzooidal boundaries indicated by thin irregular suture lines that are difficult to see by light microscopy. Frontal shield centrally imperforate with numerous, fairly conspicuous areolar pores; these generally in one row around the margins but in places encroach 2–3 deep onto the frontal shield. Primary orifice sunken, with the distal oral shelf visible at a deeper level; secondary orifice generally a little wider (0.15–0.19 mm) proximally than distally, the proximal rim concave, gently convex, or more or less straight, generally with a spine base visible on each side. Secondary orifice cormidial, the distal rim being contributed by 1–2 distal zooids whose proximal edges descend to distal rim of primary orifice, above which is often a pair of areolar pores. Larger pores/foramina in frontal shield, either laterally, proximally, or interzooidally, have an inwardly sloping rim surrounding a central opesia – these are interpreted to be kenozooids or simple avicularia. Ovicells not seen.

REMARKS. This species accords well with the characters of *Hippopleurifera*, as exhibited by the range of species attributed to this genus. The type species (clarified by Hastings 1966), *H. biauriculata*, has multiple areolar pores that give the frontal shield a more porous appearance than in most of the other species in the genus, but otherwise shield structure is probably umbonuloid in all of them. According to published descriptions, the type species lacks oral spines, but these are present in Recent *H. pulchra* (Manzoni) and several fossil species (Hastings 1949; Cheetham 1966). The genus is well represented in the European Tertiary, with as many as nine species occurring in the Badenian (Langhian-Serravallian) of Austria alone (Vávra 1977). The earliest-known occurrence of the genus was that of *H. canui* Cheetham, 1966 from the Lutetian of Sussex and southwest France, now antedated by *H. australis*, which is also the first record of the genus from the Southern Hemisphere.

### Genus ***EXOCHELLA*** Jullien, 1888

TYPE SPECIES. *Mucronella tricuspis* Hincks, 1881; Recent, Australia.

### ***Exochella*? *gracilis*** sp. nov. Figs 100, 101

HOLOTYPE. IGNS BZ 200, a single fragment from Pukekio, Chatham Island.

NAME. From the Latin *gracilis*, slender, referring to the erect, gracile colony form.

DESCRIPTION. Colony erect, forming gracile, bilamellar stems 0.80–1.23 mm wide, lensoidal in cross-section. Autozooids alternate in 2 longitudinal series on each side of the stem, separated by another series along each margin; length = 0.64–0.76 mm, width = 0.35–0.47 mm. Frontal shield increasing in convexity from the proximal end towards the orifice, the surface relatively smooth with 6–7 conspicuous areolar pores along each margin and 1–3 proximally. Orifice obscured by sediment, wider (0.18–0.22 mm) than long, the proximal rim possibly straight or gently concave. No oral spines. In some zooids, one of the midlateral areolar pores is larger than the others with an inwardly sloping rim surrounding an oval foramen; it appears to be directed outwards laterally and may be an avicularium. No ovicells present.

REMARKS. Owing to occlusion of the orifice by sediment particles it is difficult to be certain concerning generic and even familial attribution. The presence of a very convex frontal shield suborally and an apparent lateral avicularium allows inclusion in the Romancheinidae and possibly the genus *Exochella* (cf. Hayward 1995: Fig. 137E). More material is needed for confirmation.

### Genus ***ESCHAROIDES*** Milne Edwards, 1836

TYPE SPECIES. *Cellepora coccinea* Abildgaard, 1806; Recent, North Atlantic.

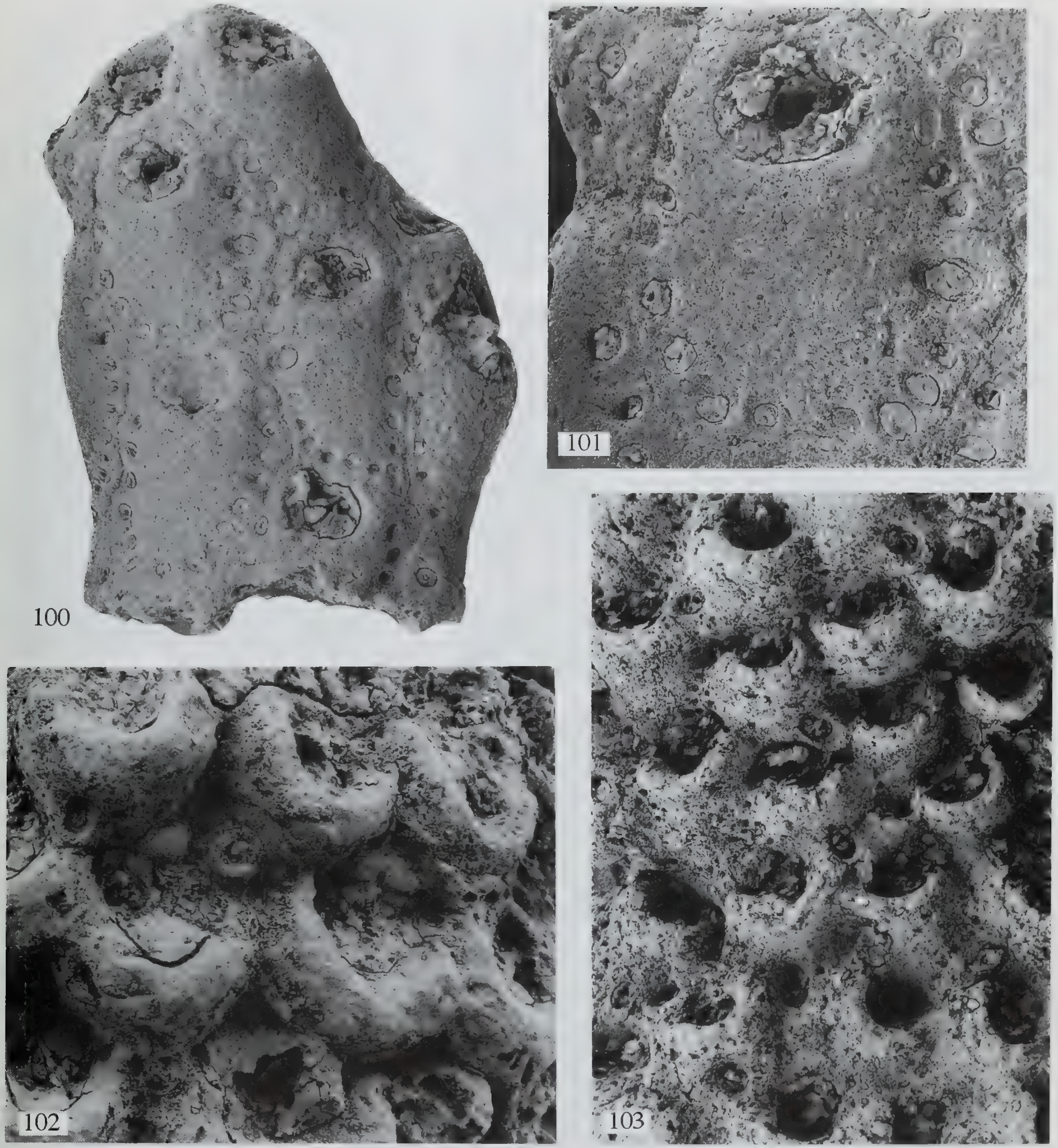
### ***Escharoides*? *crassa*** sp. nov. Figs 102, 103

HOLOTYPE. IGNS BZ 201, from Pukekio Hill, Chatham Island.

PARATYPE. NHM BZ 4787.

NAME. From the Latin, *crassus*, thick, referring to the thick frontal shield and peristome.

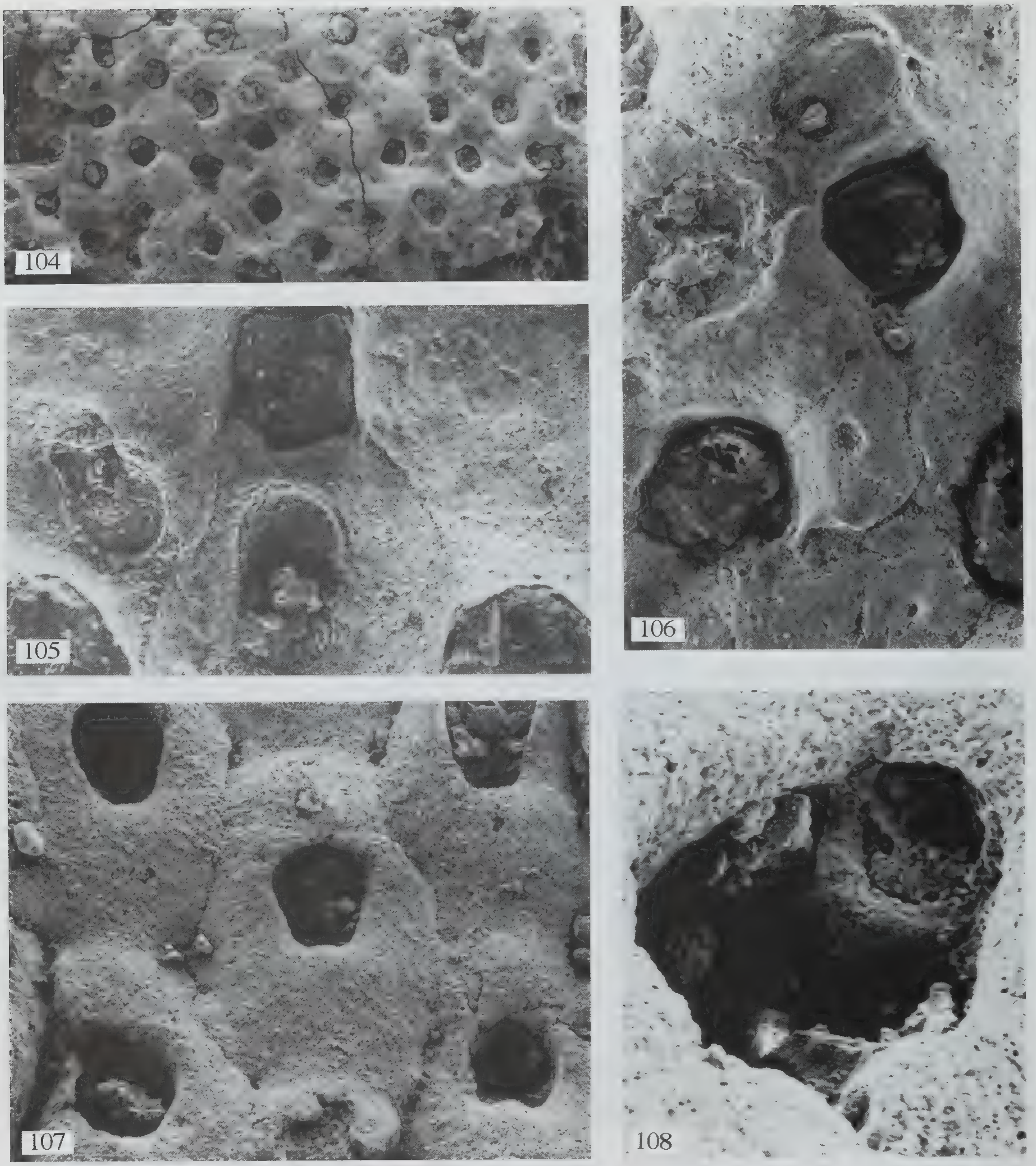
DESCRIPTION. Colony encrusting. Autozooids robust, length = 0.65–0.84 mm, width = 0.50–0.67 mm. Frontal shield thick-walled, imperforate except for marginal areolar pores, rising to the broadest



**Figs 100–103** Romancheinid cheilostomes. **100–101,** *Exochella*? *gracilis* sp. nov., IGNS BZ 200, **holotype**; **100,** zooids in bilamellar fragment, × 62; **101,** autozooid; probable avicularium at middle right of zooid, × 124. **102–103,** *Escharoides*? *crassa* sp. nov., IGNS BZ 201, **holotype**; **102**, disposition of thick-peristomed autozooids and adventitious avicularia, × 54; **103**, × 30.

part of the zooid where there is a high scoop-like peristome that surrounds a more-or-less distally facing secondary orifice. Primary orifice occluded by sediment, details not known. No oral-spine bases. Frequently an avicularium adjacent to one corner of the peristome, 0.18–0.24 mm long, elongate-oval with a rounded rostrum that slopes steeply inwards to a narrow palate, the avicularium not as wide proximally; the preservation is inadequate to indicate whether there may have been a crossbar. Ovicells not present.

REMARKS. The generic attribution is uncertain. The species is most reminiscent of Recent *Escharoides angela* (Hutton, 1873) which also has a conspicuous scoop-like peristome. The origin of the



**Figs 104–108** Ascophoran cheilostomes. **104–106**, Lepraliellid sp. 1, IGNS BZ 217; **104,** disposition of autozooids, × 32; **105,** lingulate adventitious avicularia and adjacent zooidal orifices, × 193; **106,** zooidal orifices and a concavity probably indicating the position of a former hyperstomial ovicell, × 154. **107–108,** *Chataimulosia primaeva* sp. nov., IGNS BZ 202, **holotype**; **107,** ovicelled zooids, × 112; **108,** peristomial orifice, showing median suboral avicularium with crossbar, and position of primary orifice at a deeper level, × 470.

avicularium in *E. crassa* is equivocal, however. In species of *Escharoides*, one or a pair of lateral-oral avicularia occurs adjacent to the peristome. In the present material the single avicularium could have been budded from an areolar septula pore adjacent to the peristome or, what appears more likely, from a septular pore in the proximal part of the shield of the distal zooid. *Escharoides* species typically have oral spines but there is no trace of oral-spine bases in the poorly preserved material at hand.

## Family **LEPRALIELLIDAE** Vigneaux, 1949

### Genus ***INCERTAE SEDIS***

***Lepraliellid*** sp. 1 Figs 104–106

MATERIAL. IGNS BZ 217, from Pukekio, Chatham Island.

DESCRIPTION. Colony encrusting. Autozooids porcellanous, arranged somewhat irregularly with no discernible boundaries and even zooidal orientation is somewhat difficult to determine; length ca. 0.43 mm. Frontal shield convex, smooth-surfaced, imperforate except for tiny, sparsely distributed pores assumed to communicate with areolar septular pores. Peristomial orifice irregular in shape, often as wide as long and subrounded, the primary orifice occluded and concealed. No oral spine bases. Avicularia sparsely distributed, relatively large and more or less lingulate, the broad, rounded rostrum slightly broadening distally and with an extensive flat palate; there is a relatively large central foramen where the avicularium is slightly indented, and a narrow opesial shelf proximally; no evidence of a crossbar or distinct mandibular pivots. No complete ovicells present, but an excavation distal to one orifice appears to represent the inner endooecial surface of a hyperstomial ovicell unable to have been closed by the zooidal operculum.

REMARKS. The generic affinities of the sole specimen are presently indeterminable.

***Lepraliellid*** sp. 2 Figs 109, 110

MATERIAL. NHM BZ 4788, IGNS BZ 218, two 'bryoliths' from Pukekio, Chatham Island.

DESCRIPTION. Colony self-encrusting, multilamellar, forming free 'bryoliths' around a presumed nucleus (a small gastropod shell evident in one eroded colony). Autozooids relatively small, arranged irregularly, with merging boundaries; length = 0.33–0.37 mm, width = 0.28–0.30 mm. Frontal shield convex, more-or-less smooth-surfaced, imperforate except for 8–9 conspicuous areolar pores around the margin. Peristomial orifice about as wide as long (both 0.09–0.10 mm), the lateral margins continuous with the sides of a median suboral avicularium (broken in all zooids), the primary orifice at a deeper level and apparently with a straight proximal margin. Distal oral spine bases not readily apparent. Chamber of suboral avicularium broad, extending to a septular pore on either side. Ovicells not identifiable.

REMARKS. Only the larger of the two colonies is sufficiently well-preserved to show details of zooidal morphology. In overall appearance the colony and zooids are very typical of celleporids and many lepraliellids. The species is not determinable to genus, however, and is provisionally included here in the Lepraliellidae on the basis of the apparently straight proximal rim of the primary orifice. The lack of an orificial sinus suggests that the frontal shield might be umbonuloid in structure.

## Family **BUFFONELLODIDAE** Gordon & d'Hondt, 1997

### Genus ***CHATAIMULOSIA*** gen. nov.

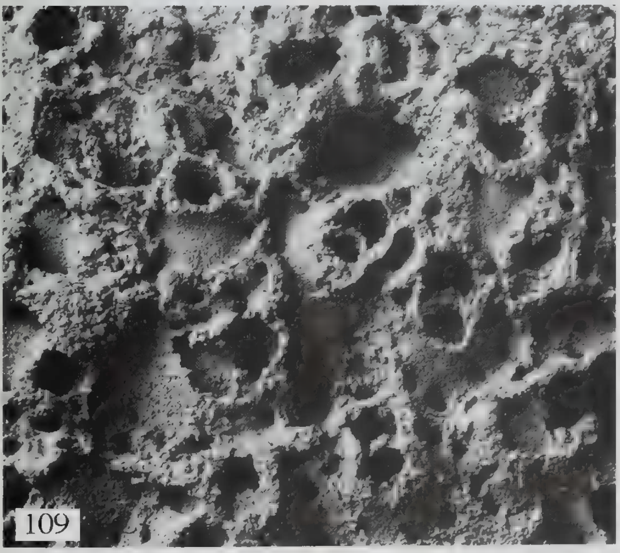
TYPE SPECIES. *Chataimulosia primaeva* sp. nov., by monotypy; latest Teurian-Waipawan (latest Thanetian (earliest Ypresian), Chatham Island, New Zealand.

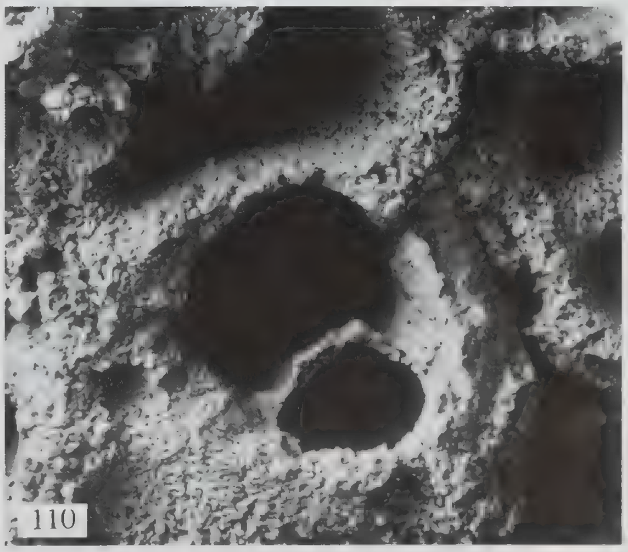
DIAGNOSIS. Colony encrusting. Autozooids with a smooth, imperforate frontal shield lacking areolar septular pores. Primary orifice sunken, the proximal rim straight, lacking a lyrula or denticle. Secondary orifice with a median suboral avicularium with crossbar. No oral spines. Ovicell hyperstomial, recumbent, smooth and imperforate with its calcification merging into that of the succeeding frontal shield.

NAME. A combination of Chatham and *Aimulosia*, a genus of Buffonellodidae.

***Chataimulosia primaeva*** sp. nov. Figs 107, 108

HOLOTYPE. IGNS BZ 202, from Pukekio, Chatham Island. No paratypes.





**Figs 109–110** Lepraliellid sp. 2, NHM BZ 4788; **109**, zooids visible on abraded colony surface, × 70; **110**, secondary orifice and chamber of median suboral avicularium, × 300.

NAME. From the Latin *primaevus*, early, alluding to the earliest occurrence of the genus and family.

DESCRIPTION. Colony encrusting. Autozooids arranged regularly quincuncially, the interzooidal boundaries indicated by thin suture lines; length = 0.46–0.56 mm long, width = 0.22–0.36 mm. Frontal shield centrally imperforate, rather smooth, with no apparent areolar pores. Primary orifice somewhat sunken, the proximal rim more-or-less straight without either sinus or median convexity. Secondary orifice in most zooids longer than wide with a small, semi-concealed suboral avicularium below its proximal rim; avicularium circular with a complete crossbar. No oral spines. Ovicell hyperstomial, somewhat recumbent on the succeeding zooid, the external surface smooth and imperforate, the proximal margin defined by extensions of the lateral zooid margins that pass across it; secondary orifice of ovicellate zooids subpyriform.

REMARKS. This monotypic genus shares a number of characters with Miocene-Recent *Aimulosia* Jullien, 1888 (see Gordon 1989b; Hayward & Thorpe 1990). Significant differences include the lack of marginal areolar pores, sunken primary orifice, lack of median lyrula or denticle, lack of oral spines, and extensions of the lateral wall that cover the proximal rim of the ovicell. Collectively, these are deemed adequate for the recognition of a new genus. *Chataimulosia primaeva* is the earliest-known species of the austral family Buffonellodidae.

## DISCUSSION

Paleogene southern hemisphere bryofaunas are relatively poorly known so the likelihood of range extensions and new taxa is correspondingly high. Such is the case with the Red Bluff Tuff Bryozoa. Of the 22 species with characters adequate for the application of species names, 21 are new and the remaining species is equivocal, hence local and regional endemism are very high. Three genera are new – *Melychocella*, *Smitticellaria* (Cellariidae) and *Chataimulosia* (Buffonellodidae), the latter comprising the earliest occurrence of the Buffonellodidae, the only family in the collection representative of a 'cryptocystidean' frontal shield. Forward range extensions include *Flustrellaria*, *Inversaria*, and possibly *Escharicellaria* and *Pavobeisselina*. Backward range extensions include *Cinctipora* and Cinctiporidae (discounting the possible *Cinctipora* from the Late Cretaceous of South Africa), and *Akatopora*. Newly recorded for the southern hemisphere are *Flustrellaria*, *Inversaria*, *Hippopleurifera*, and possibly *Hoplitaechmella*, *Escharicellaria* and *Pavobeisselina*.

The overall taxonomic character of the bryofauna is mixed, both geographically and temporally, with genera reminiscent of northern hemisphere Maastrichtian and Danian bryofaunas co-occurring with families like Arachnopusiidae and Romancheinidae that are common in Neogene and Recent southern hemisphere bryofaunas. As with molluscs (Stilwell 1997), the Red Bluff Tuff bryofauna appears to bear little relationship to the bryofauna of the Late Cretaceous Kahuitara Tuff (Taylor 1996) which directly underlies it on Pitt Island.

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